

THE OSTEOLOGY OF *NOTELOPS*
WOODWARD, *RHACOLEPIS* AGASSIZ AND
PACHYRHIZODUS DIXON (PISCES: TELEOSTEI)

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SYNOPSIS

The osteology of representative species of the Cretaceous teleosts *Notelops* Woodward, *Rhacolepis* Agassiz and the English species of *Pachyrhizodus* Dixon is described. *Thrissopater* Günther is placed in synonymy with the genus *Pachyrhizodus*. *Notelops*, *Rhacolepis* and *Pachyrhizodus* are considered to form a monophyletic group based on the common possession of patterns of derived character states in the circumorbital series and the caudal skeleton. The suborder Pachyrhizodontoidae is erected to contain these genera. The complement of derived character states shown by the pachyrhizodontoids is comparable with that shown by

protacanthopterygian euteleosts, in particular with the salmonoids. However, as neither the Euteleostei nor the Protacanthopterygii can, as yet, be defined, the Pachyrhizodontoidei are left as Teleostei *incertae sedis*. *Rhacolepis* and *Pachyrhizodus* are grouped together in the family Pachyrhizodontidae Cope. *Notelops* is placed in a new family Notelopidae and stands as the plesiomorph sister-group of the Pachyrhizodontidae.

I. INTRODUCTION

THIS PAPER is concerned with the osteology of the Cretaceous teleosts *Notelops* Woodward, *Rhacolepis* Agassiz, *Thrissopater* Günther and *Pachyrhizodus* Dixon. A few notes are added concerning the lesser known genus *Elopopsis* Heckel. At the time of writing Ms S. Teller, of the Department of Biology, University of Illinois at Chicago Circle, is undertaking a review of the North American species of *Pachyrhizodus* and consequently only the English species of *Thrissopater* and *Pachyrhizodus* are treated in detail in the present paper. The work arises from a broader study on the fishes included by Woodward (1901) in the families Elopidae and Albulidae. Part of the results have been published (Forey 1973a, b) and revisions of *Spaniodon* and *Thrissopteroideis* will be published elsewhere.

The genera to be dealt with here were included by Woodward (1901) in the family Elopidae. Within the Elopidae Woodward (1901: 7-8) recognized, in the form of a key, two groups of genera. One of these groups, later termed the 'elopine group' by Dunkle (1940), is characterized by showing medially united parietals and includes *Notelops* and *Elopopsis* of the fishes to be dealt with here. The other group, the 'spaniodontine group' of Dunkle (1940), shows separated parietals and includes *Rhacolepis*, *Thrissopater* and *Pachyrhizodus*. This separation of *Notelops* from *Rhacolepis*, *Thrissopater* and *Pachyrhizodus* appears to have been followed by most subsequent workers, some of whom have placed the latter genera in a separate family or families.

Notelops Woodward and *Rhacolepis* Agassiz are known only from the Santana Formation of the Araripe plateau, Ceará, Brazil. This formation is reputed to be Aptian in age and to represent an estuarine deposit (Santos & Valença 1968; Mabe-soone & Tinoco 1973). The anatomy of *Notelops* was briefly described by Woodward (1887, 1901), Jordan (1907, 1921) and Jordan & Branner (1908). Dunkle (1940) described, in great detail, the cranial osteology of *Notelops*, his description being based on the serial sectioning of a single specimen. I have been able to check this description against several acid-prepared specimens and have added information; the postcranial skeleton has never been examined in detail hitherto. *Notelops* has always been placed in the family Elopidae with the recognition that it is closely related to *Elops*. Thus Dunkle (1940: 187) wrote: '*Elops* can be regarded as an unmodified descendant of a form closely related to *Notelops*'. To date, this statement remains unchallenged.

Elopopsis Heckel is a genus known by several species from the Cenomanian of Jugoslavia, Czechoslovakia, Morocco, the Turonian of England and the Campanian of Westphalia. None of the species is particularly well known. *Elopopsis* was first classified (Woodward 1901) as an 'elopine elopid' but the probable separation

of the parietals (Woodward 1908) should have placed it in the 'spaniodontine group'. Applegate (1970) places *Elopopsis* in association with *Thrissopater*, *Pachyrhizodus* and *Rhacolepis* in the superfamily Pachyrhizodontoidae, comprising the single family Pachyrhizodontidae Cope.

Brief descriptions of *Rhacolepis* have been given by Woodward (1887, 1901), Jordan (1921) and Jordan & Branner (1908). The availability of several specimens that could be prepared in acid has resulted in an almost complete description of the osteology. *Rhacolepis* was placed in the Elopidae by Woodward (1901) although both that author and several others (Dunkle 1940, Applegate 1970 and Santos & Valenca 1968) have recognized that it is morphologically more similar to *Thrissopater* and *Pachyrhizodus* than to *Notelops*.

Thrissopater Günther is represented by two species from the Cretaceous of England, *T. salmoneus* Günther from the Albian and *T. megalops* Woodward from the Cenomanian. Each of these species is known by only a handful of specimens. I can add little to the descriptions of *T. salmoneus* given by Günther (1872) and Woodward (1901). A specimen of *T. megalops* was prepared in acetic acid and used as the basis for a detailed description of the cranium. During the course of this work it became apparent that there were no significant differences between the genera *Thrissopater* and *Pachyrhizodus* and it is suggested that *Thrissopater* be included within the genus *Pachyrhizodus*. However *Thrissopater daguini* Arambourg (1954), from the Cenomanian of Morocco, shows little resemblance to other species of *Thrissopater*.

Thrissopater has been considered as a 'spaniodontine elopid' by Woodward (1901) and Dunkle (1940). Jordan (1905) included *Thrissopater* with *Spaniodon* in the family Spaniodontidae, a family which was thought to be closely related to the Elopidae. Boulenger (1910) placed *Thrissopater* as a monogeneric subfamily, the Thrissopatrinae, in the family Clupeidae, stating that this genus is a link between the Elopidae and the Clupeidae. Bertin & Arambourg (1958: 2214) recognized *Thrissopater* as very similar to *Pachyrhizodus* and placed both in the family Thrissopateridae. The Thrissopateridae were placed in the suborder Elopoidei together with the Elopidae, Albulidae and Pterothrissidae.

Pachyrhizodus Dixon is known from marine Cretaceous deposits of England, North America and Australia. The English species, represented mostly by cranial fragments, have been excellently described by Woodward (1901, 1907, 1908, 1911). The North American species have received attention in works by Stewart (1898, 1899), Loomis (1900), Hay (1903), Cope (1874, 1875) and Applegate (1970). *Pachyrhizodus marathonsensis* (Etheridge) from Australia is most completely described by Bartholomai (1969).

Pachyrhizodus is the type genus of the family Pachyrhizodontidae Cope. Cope (1872) included within the family other genera that are probably synonymous with *Pachyrhizodus*, and placed the Pachyrhizodontidae in association with the Saurodontidae and the Ichthyodectidae. Later Cope (1875) abandoned the Pachyrhizodontidae and placed *Pachyrhizodus* with *Stratodus* Cope and *Cimolichthys* Leidy in the family Stratodontidae. Fowler (1911) erected the family Raphiosauridae, based on the mistaken assumption that *Raphiosaurus* was the senior synonym of *Pachyrhizodus*. Jordan (1923) maintained the Raphiosauridae (= Pachyrhizodontidae)

to include eleven genera, nine of which are junior synonyms of *Pachyrhizodus*, while the remaining genus, *Anogmius* Cope (= *Bananogmius* Whitley, *Ananogmius* White & Moy-Thomas), is now regarded as a tselfatioid (Patterson 1967). Loomis (1900) and Stewart (1899) referred *Pachyrhizodus* to the Salmonidae. Boulenger (1910) also mentioned the Pachyrhizodontidae with the Salmonidae, although he expressed doubts concerning the systematic position of *Pachyrhizodus*. Woodward (1901) and Dunkle (1940) considered *Pachyrhizodus* as a 'spaniodontine elopid' and more recently it was placed with *Thrissopater* in a family separate from the Elopidae by Bertin & Arambourg (1958) and Applegate (1970). In considering the lower jaw structure of the American species of *Pachyrhizodus* Nelson (1973a) placed the genus as Teleostei *incertae sedis*.

The brief notes above concerning the history of the classification of these genera reveal two main points. Firstly, it is generally believed that *Notelops* is closely related to *Elops* whereas the other genera are removed from this lineage. Secondly, although *Rhacolepis*, *Thrissopater* and *Pachyrhizodus* may be separated from *Notelops* and *Elops* at the family level, the consensus of opinion favours placing the former genera near to the Elopidae with the implication that elopids are their nearest relatives.

My studies on the osteology of *Notelops*, *Rhacolepis*, *Thrissopater* and *Pachyrhizodus* suggest that these genera form an interrelated group of primitive teleosts that are very different from the elopids. These genera show several points of similarity with the protacanthopterygians, but there is insufficient evidence to justify their inclusion within that assemblage and they are left as Teleostei *incertae sedis*.

II. MATERIALS AND METHODS

Material used in the preparation of this work is in the collections of the British Museum (Natural History), London; Institute of Geological Sciences (Geological Survey Museum), London; Sedgwick Museum, Cambridge; University of Alberta (Geology Department); American Museum of Natural History, New York; and Southern Methodist University, Dallas, Texas. Specimens belonging to these institutions are identified by register numbers with the prefixes BM(NH), GSM, SM, UA, AMNH and SMU respectively.

Several specimens of *Notelops* and *Rhacolepis* were prepared by the transfer technique (Toombs & Rixon 1959). One specimen each of *Pachyrhizodus megalops* and *P. subulidens* were prepared in acetic acid as 'free-standing' specimens.

III. SYSTEMATIC DESCRIPTIONS

Suborder PACHYRHIZODONTOIDEI *nov.*

DEFINITION. Primitive teleostean fishes, fusiform with terminal mouths and large jaws; frontals large, dermethmoid large, parietals small, parietal branch of supraorbital sensory canal absent, nasals short and tubular, supraoccipital small with weakly developed crest; supratemporal large; post-temporal fossa roofed;

orbitosphenoid and basisphenoid present, occipital condyle formed entirely by basioccipital, saccular region of neurocranium not inflated, parasphenoid without teeth or basipterygoid process, foramen for buccohypophyseal canal present; hyomandibular with single articulatory head, hyomandibular held vertically, endopterygoid with many small teeth, palatine without maxillary process; anterior and posterior ceratohyals separated by a narrow band of cartilage, numerous branchiostegal rays present; premaxilla with small dorsal process, one or two inner teeth and a single row of marginal teeth; maxilla long and shallow with a simple head fitting tightly against the premaxilla, a single splint-like supramaxilla, a single row of maxillary teeth; mandibular ramus shallow with a well-developed postarticular process, dentary and angular showing a 'reverse overlap'; large supraorbital meeting a large dermosphenotic, no separate antorbital, second and third infraorbitals fused together, posterior branch of infraorbital sensory canal within the dermosphenotic; two sclerotic ossicles; opercular apparatus complete; meso-coracoid present; pectoral fin held low on flank, pectoral splint absent; pelvic fins abdominal; vertebral centra pierced by notochordal canal, neural arches fused with centra except in anterior half of abdominal region, posterior parapophyses and haemal arches fused with centra, epineurals fused to neural arches, pleural ribs curved, supraneurals behind occiput; dorsal and anal fins acuminate, always distinct from caudal fin; caudal fin forked with 19 principal fin-rays; parhypural and lower hypurals fused to supporting centra, half-length neural spine on second preural centrum, first uroneural large, second uroneural reaching to first ural centrum, second ural centrum small, two epurals; scales cycloid with bone-cell spaces; lateral line complete.

Family **NOTELOPIDAE** *nov.*

DIAGNOSIS. Pachyrhizodontoid fishes in which the skull roof is flat, ethmoid commissure bone enclosed, frontal margin not excavated, parietals medially united; subtemporal fossa present, intercalar large and extending anteriorly to form a prootic-intercalar bridge, trigeminal foramen opening into pars jugularis, myodome closed posteriorly, parasphenoid shallow beneath otic region; palatine long and dentigerous, ectopterygoid edentulous; lower jaw with separate angular, articular and retroarticular; dentary with several rows of teeth; gular plate present.

Genus **NOTELOPS** Woodward 1901

DIAGNOSIS (emended). Notelopid fish in which the dermethmoid bears lateral projections, dilatator fossa with roof, pterotic without posterior spine, exoccipitals meeting above and below foramen magnum, large fenestra between autosphenotic and pterotic, lateral face of prootic without a crest above the orbitonasal foramen; anterior ceratohyal fenestrated; fourth and fifth infraorbitals fused together, posterior infraorbitals just reaching the preoperculum; preoperculum relatively small, operculum with oblique ventral margin, interoperculum short and deep; cleithrum expanded over fin insertion; origin of pelvic fin below posterior end of

dorsal fin, pelvic splint-bone present; upper principal caudal fin-rays crossing hypural supports at a steep angle; scales small, marked by evenly spaced circuli around a central focus, a few scales extending over the base of the caudal fin.

TYPE SPECIES. *Rhacolepis brama* Agassiz.

Notelops brama (Agassiz)

(Figs 1-10)

- 1833 *Amblypterus olfersi* Agassiz, 2: 40.
 1841 *Phacolepis brama* Agassiz: 83.
 1841 *Calamopleurus cylindricus* Agassiz: 84.
 1844 *Rhacolepis olfersii* (Agassiz); Agassiz, 4: 293.
 1844a *Rhacolepis olfersii* (Agassiz); Agassiz: 1012.
 1887 *Rhacolepis brama* Agassiz; Woodward: 539; pl. 46, fig. 1; pl. 47, fig. 4.
 ? 1895 *Calamopleurus cylindricus* Agassiz; Woodward: 499.
 1901 *Notelops brama* (Agassiz) Woodward: 27.
 1907 *Calamopleurus cylindricus* Agassiz; Jordan: 139; pl. 12.
 1908 *Calamopleurus cylindricus* Agassiz; Jordan & Branner: 16; pl. 3.
 1908 *Notelops brama* (Agassiz); Jordan & Branner: 20; pl. 6, fig. 1.
 1921 *Calamopleurus brama* (Agassiz); Jordan: 46; pl. 5, figs 1, 2; pl. 6, figs 1-3; pl. 7, figs 1-3.
 1938 *Notelops brama* (Agassiz); D'Erasmus: 349.
 1940 *Notelops brama* (Agassiz); Dunkle: 157.
 1968 *Notelops brama* (Agassiz); Santos & Valença: 348, fig. 6.

DIAGNOSIS (emended). *Notelops* reaching 600 mm total length; proportions (as percentage of standard length): head length 25, maximum depth of trunk 20-21, predorsal 46-49, prepelvic 55-58, preanal 78-80; fin-ray counts, D. iv, 11 or 12; A. ii, 6; P. 15-17; V. 12 or 13; approximately 60 preural vertebrae of which 19 or 20 are caudal; premaxilla equal to 22 per cent of length of upper jaw, with about 18 marginal teeth; maxilla with about 50 teeth; dentary with 3-4 rows of teeth, each row containing approximately 60 teeth; preopercular sensory canal with 3-5 ventral branches; diameter of orbit equal to 25 per cent of head length; 90-100 lateral line scales, 25-27 scales in transverse series anterior to dorsal fin, large axillary scale above pectoral fin.

HOLOTYPE. BM(NH) 15490, head plus cleithrum, Santana Formation (Aptian), Ceará, Brazil.

MATERIAL. Nineteen specimens in the British Museum (Natural History), four in the University of Alberta and one in the American Museum of Natural History were examined.

FORMATION AND LOCALITY. Not all specimens bear locality data but the distinctive matrix and preservation suggest that all come from the Santana Formation (Aptian), Ceará, Brazil.

DESCRIPTIVE REMARKS. Dunkle (1940) presents a detailed account of the cranial osteology of *Notelops brama*, his description being based on serial sections of a single specimen. The following notes are based on several acid-prepared specimens

and are intended to supplement or correct the description given by Dunkle. A description of the postcranial skeleton is also given.

Braincase. A comparison of Fig. 1 with that given by Dunkle (1904: fig. 1A) shows a general similarity between the two reconstructions. I find the medially united parietals to be small and to have irregular margins. The path of the supra-orbital sensory canal is shown in Fig. 1. The supraorbital sensory canal opens medially by two large pores. Posterolaterally the canal opens by several pores above the autosphenotic. There is no parietal branch or any evidence of pit-lines such as are seen in *Elops*.

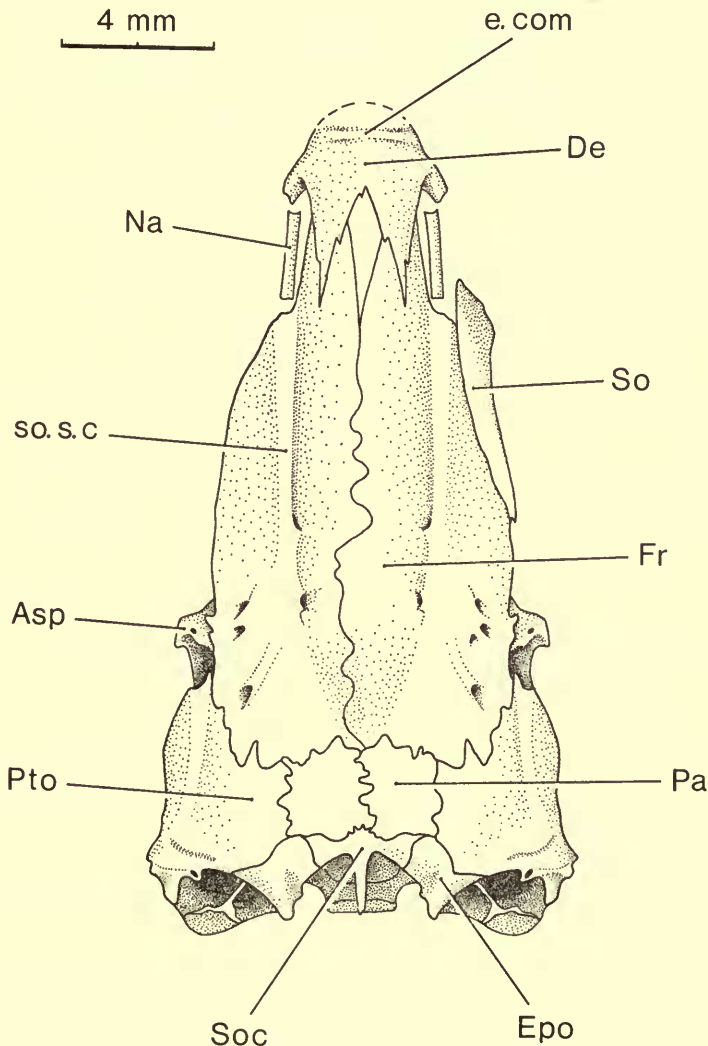


FIG. 1. *Notelops brama* (Agassiz). Restoration of braincase in dorsal view.

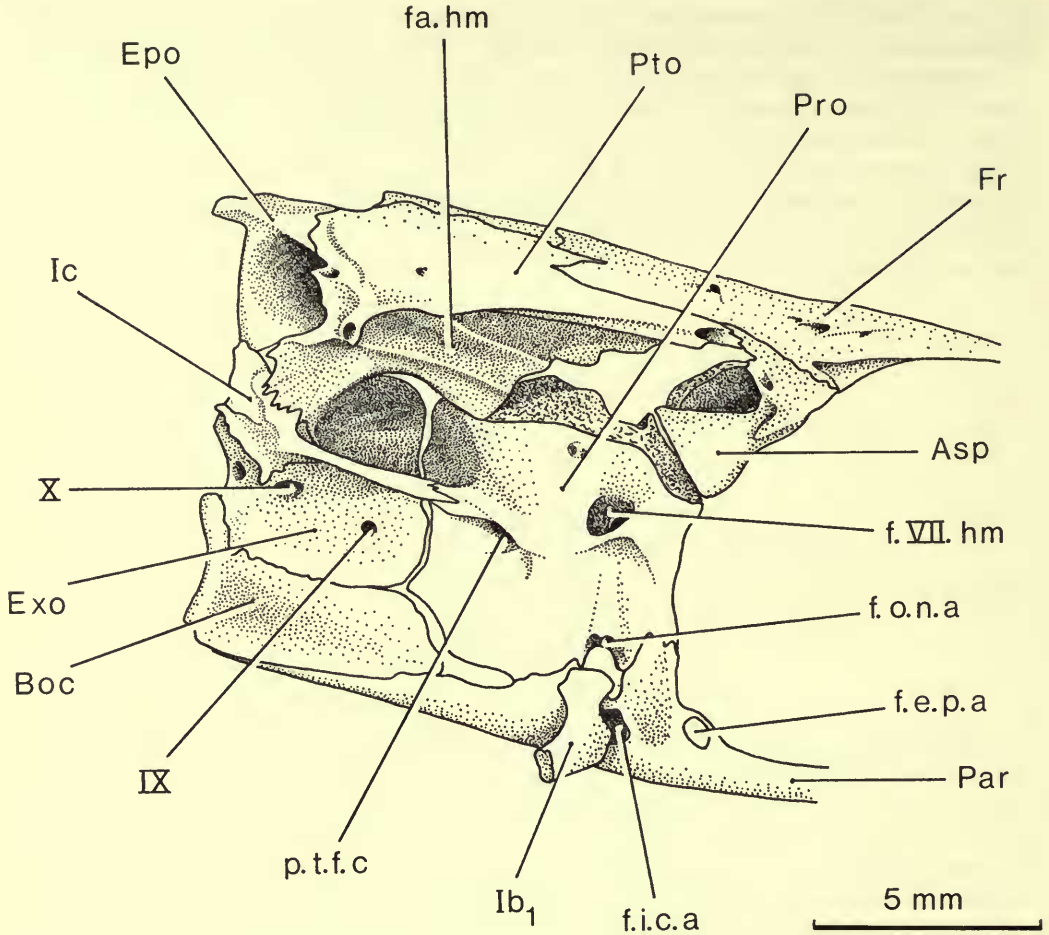


FIG. 2. *Notelops brama* (Agassiz). Postorbital part of braincase in right lateral view. Camera lucida drawing of UA 12021, a young individual.

Dunkle makes no mention of the foramen for the exit of the glossopharyngeal; it occurs in the usual position, on the lateral face of the exoccipital beneath the subtemporal fossa (Fig. 2, IX).

The intercalar (Fig. 2, Ic) is large, with an anteriorly directed strut which interdigitates with a ridge on the prootic, forming a prootic-intercalar bridge as in *Elops* and *Leptolepis dubia* (Blainville).

In the lateral face of the prootic Dunkle (1940: 175, figs 1c, 5b) notes that the posterior palatine branch of VII left the prootic by a foramen which is separate from the foramen for the orbital artery. Bardack (1965: 43) also notes a separate foramen in *Xiphactinus audax* Leidy. In BM(NH) P.1958 and UA 12021 there is no such separate foramen and presumably the posterior palatine branch of VII and

the orbital artery shared a single foramen (Fig. 2, f.o.n.a). The presence of a single or double foramen is probably subject to individual variation.

The path of the abducens nerve, as reconstructed by Dunkle (1940 : fig. 6), is shown passing over the floor of the endocranial cavity to descend into the posterior myodome through the pituitary fossa. Such a path is unusual among 'lower teleosts'. All specimens examined here show a foramen within the prootic bridge, suggesting that the abducens followed a more usual course, directly through the floor of the endocranial cavity.

A feature worthy of note is the presence of a large fenestra between the autosphenotic and the pterotic (Fig. 2), in the wall of the dilatator fossa. This fenestra is present in all specimens examined. The margin of this fenestra in the largest specimen (UA 12020) is 'finished', suggesting an open area or one perhaps covered by membrane. If open, there was direct communication between the dilatator fossa and the post-temporal fossa. Similar fenestrae are seen in some specimens of *Tarpon atlanticus* (Cuvier & Valenciennes), *Brycon meeki* Eigenmann & Hildebrand (Weitzman 1962) and *Scleropages formosus* (Müller & Schlegel) (personal observation). The function of these fenestrae is not known.

On the orbital face there is a large, slit-like foramen straddling the suture between the autosphenotic and the pterosphenoid. The long axis of this foramen is inclined dorsomedially. The foramen leads from the orbit to the post-temporal fossa. A groove passes from the ventral lip of this foramen to the anterior opening of the jugular canal. The position of this foramen and the presence of the groove suggests that the ramus lateralis accessorius nerve ran up the orbital face and through the foramen. A smaller foramen, of unknown function, leading to the post-temporal fossa is seen within the pterosphenoid, close to the suture with the autosphenotic. The dorsal surface of the autosphenotic contains a small foramen (Figs 1, 2) which may have carried the otic branch of VII. It is not apparent where the otic nerve entered the autosphenotic, unless it ran into the bone with the ramus lateralis

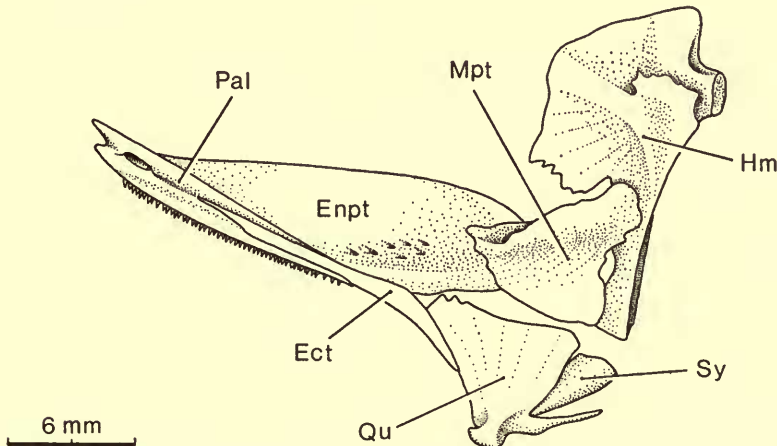


FIG. 3. *Notelops brama* (Agassiz). Left hyopalatine series in lateral view. Restoration based on UA 12021, a young individual.

accessorius. Dunkle (1940: 175) suggests that the otic branch ran out of the braincase on the lateral face of the prootic together with the hyomandibular trunk of VII.

Hyopalatine series. The hyopalatine bones (Fig. 3) have been described by Dunkle (1940: 182-184, fig. 8) but little mention was made of the dentition. The oral surface of the palatine bears many pointed teeth which are as large as those borne by the maxilla. There are 4-5 longitudinal rows of teeth. The ectopterygoid is edentulous, which is probably the result of the posterior extension of the palatine covering most of the oral surface of the ectopterygoid. The endopterygoid (entopterygoid of Dunkle 1940) bears many tiny, granular teeth which become slightly larger toward the endopterygoid/palatine interface.

Jaws. The upper jaw (Figs 4A, 6) is slender and long, reaching behind the orbit. The premaxilla (Fig. 4A, Pmx) is small and triangular and bears a ridge on the mesial surface. There are approximately 18 marginal teeth in a single row and there was probably a larger, inner premaxillary tooth anteriorly, since a socket (Fig. 4A) is seen in several specimens.

The maxilla is long and narrow, the head is simple and there is a very poorly developed palatine process. A single row of approximately 50 teeth is present.

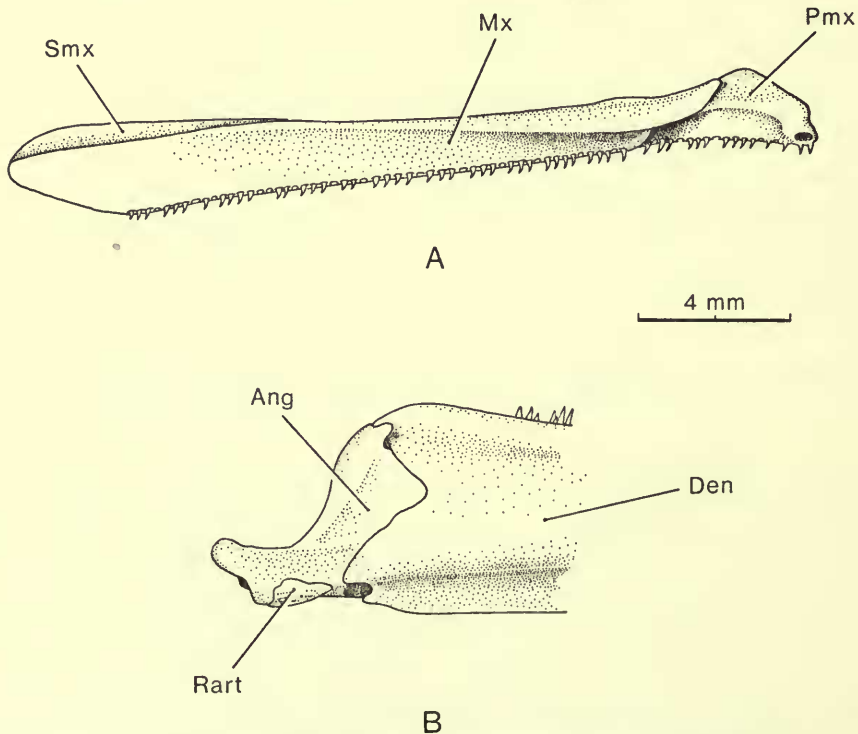


FIG. 4. *Notelops brama* (Agassiz). A: Restoration of left upper jaw in medial view. B: Posterior part of right mandibular ramus in lateral view. Camera lucida drawing of UA 12021, a young individual.

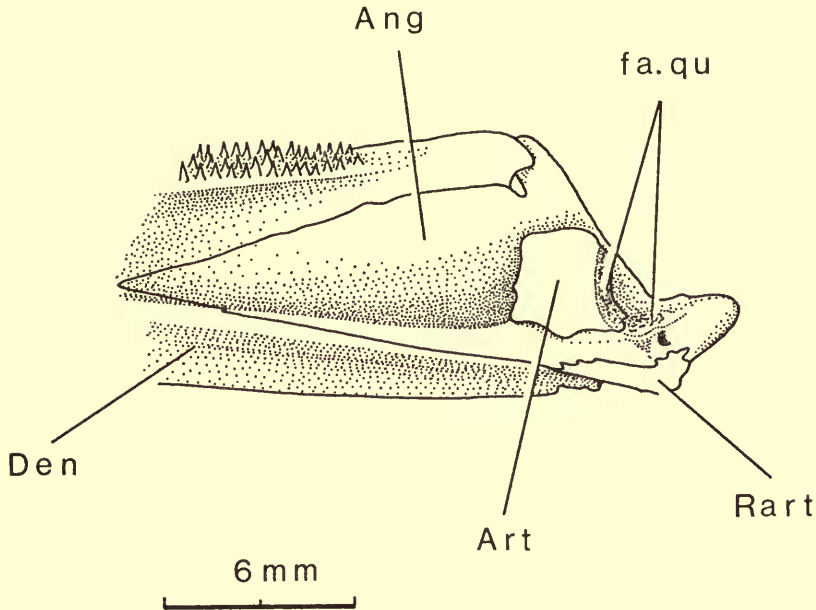


FIG. 5. *Notelops brama* (Agassiz). Posterior part of right mandibular ramus in medial view. Camera lucida drawing of UA 12022.

The bases of the teeth are fused with the maxilla and are covered laterally by a narrow ledge of thin bone. In some specimens the thin, overlapping ledge of the maxilla is broken. Hence these specimens appear to have larger teeth than those in which the ledge is complete. It may be of significance to note that Jordan & Branner (1908) distinguished *Notelops* from *Calamopleurus* (here placed in synonymy) on the supposedly larger teeth in the former.

The lower jaw (Figs 4B, 5, 6) is also long and shallow. The dentary occupies most of the mandibular length and bears a horizontal platform set with many pointed teeth. There are 3-4 longitudinal rows of teeth and, as in the maxilla, the bases of the outer teeth are covered by a narrow ledge of bone. The dentary teeth are slightly larger than those on the maxilla, being 1 mm long in a fish in which the mandible is 29 mm long. Posteriorly the angular has a small expression in lateral aspect. There is a well-developed postarticular process and a small, separate retroarticular. The angular is overlain over much of its length by the dentary, but in the region of the weakly defined coronoid process the angular portion overlaps the dentary. Nelson (1973b: 347) mentions that a similar 'reverse overlap' exists in some elopomorphs, in clupeomorphs and characoids.

The articular (Fig. 5, Art) is cuboid and rests on a ledge of the angular. The Meckelian cartilage probably lay in continuity with the anterior edge of the articular. The articular facet is divided into two parts. Most of the facet is developed on the posterior edge of the articular. The angular contributes a small horizontal portion of the facet and this lies directly behind the articular portion of the facet. The

condition in *Notelops* is similar to that described for ichthyodectids by Nelson (1973a). Both *Notelops* and the ichthyodectids have a separate articular and angular, with the articular facet developed on both bones. According to Nelson (1973a : 11) this is an unusual condition in teleosts. However, the similarity in the composition of the articular facet cannot be taken as evidence of relationship between *Notelops* and ichthyodectids, because there is the possibility that an angular component of the facet may be primitive for many lower teleosts (Nelson 1973a).

The mandibular sensory canal runs through the length of the angular and dentary. Anteriorly the canal opens by one or two pores near the symphysis ; posteriorly it opens on the posterior face of the postarticular process. There is also a small foramen on the medial face of the angular (Fig. 5) immediately behind the articular facet.

Hyoid bar, branchiostegal rays and gill arches. As usual, the ceratohyal is ossified in two sections, the anterior being the longer and having a large fenestra ('Beryciform foramen' of McAllister 1968). In some specimens the posterior ceratohyal is also fenestrated. The dorsal and ventral hypohyals are each formed of spongy bone surrounded by a thin perichondral shell. The canal for the afferent hyoidean artery enters the ventral hypohyal and leaves the dorsal hypohyal on the mesial surface.

The exact number of branchiostegal rays is not known. There were certainly more than 18. Six or seven articulate with the posterior ceratohyal. The anterior branchiostegal rays are fine, those posteriorly being only slightly expanded in comparison with those anteriorly.

The gill arches could not be reconstructed accurately. Several acid preparations show ceratobranchial, epibranchial and infrapharyngobranchial elements. One specimen shows at least two hypobranchials, but none show basibranchials or a basihyal. No basibranchial tooth plates were seen. Dunkle (1940 : 158) notes that the dorsal segments of the branchial arches were present in this specimen but makes no mention of the ventral elements. Of the gill arch elements that are ossified and preserved there is a general similarity with the generalized pattern as seen in *Elops* (Forey 1973b, Nelson 1968a). The first infrapharyngobranchial (Fig. 2, Ib₁) is closely associated with the braincase where it is attached to the parasphenoid immediately behind the foramen for the internal carotid artery. The fourth epibranchial is expanded and has a deep notch for the fourth efferent branchial artery.

Small tooth-plates are associated with the ceratobranchials and at least the first three epibranchials. There are no well-developed gill rakers.

The urohyal is long and shallow and reaches from the mid-point of the mandible to beneath the middle of the interoperculum.

Circumorbital series. This consists of a supraorbital and four canal-bearing bones. There is no separate antorbital. The supraorbital (Figs 1, 6, So) is large, sutured to the dermosphenotic posteriorly and expanded anteriorly. The first infraorbital (lacrimal of authors) is somewhat expanded anteriorly (Fig. 6, Io₁). The presence of two infraorbitals and a dermosphenotic behind the eye represents a 'reduced' condition when compared to many 'lower teleosts' (see Nelson 1969, for the generalized teleost condition).

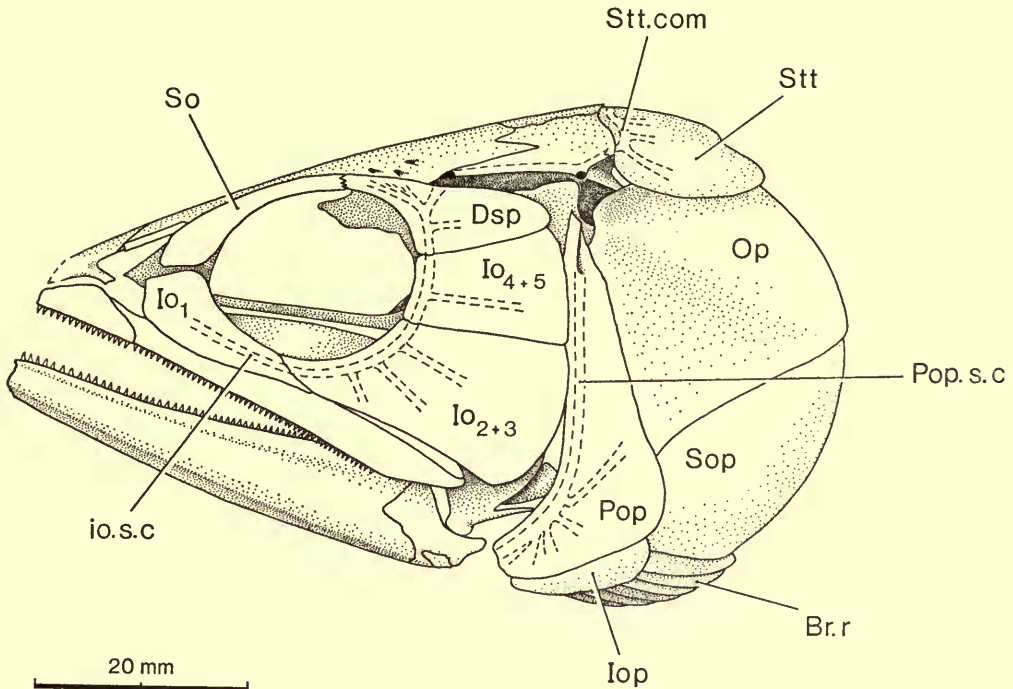


FIG. 6. *Notelops brama* (Agassiz). Restoration of cranium in left lateral view.

The large infraorbital bordering the posteroventral aspect of the orbit is interpreted as representing fused second and third infraorbitals (Fig. 6, Io_{2+3}) of a 'generalized teleost'. This interpretation is based on the size and extent of this element and the presence of three branches (hence at least three neuromasts) of the sensory canal. The two remaining posterior infraorbitals correspond to the fourth, fifth and sixth (the dermosphenotic) of a primitive teleost such as *Elops*. Thus, compared to the generalized teleost condition (Nelson 1969), the condition in *Notelops* represents one of fusion; the possibility that an infraorbital has been lost is not considered as there is no well-documented case of the loss of an infraorbital in lower teleosts. Concerning the fusion pattern, two interpretations are worth consideration—either fusion between the dermosphenotic and the fifth infraorbital or fusion between the fourth and fifth infraorbitals (Fig. 6, Io_{4+5}). Support for the first interpretation is the presence of a posterior branch in the last infraorbital (here named the dermosphenotic). However, there does not appear to be another case of a dermosphenotic fusing with a fifth infraorbital in lower teleosts (see Nelson 1969 for diagrams). Support for the second interpretation is drawn from comparisons with *Rhacolepis* (a presumed close relative of *Notelops*) where there are distinct fourth and fifth infraorbitals. In *Rhacolepis* (see p. 157 and Fig. 20) the fourth infraorbital carries a branch of the main sensory canal while the fifth is without a branch. In *Notelops* the branch is seen in the lower half of the posterior infraorbital, and the depth of this infraorbital is comparable to the combined depth of

the fourth and fifth infraorbitals in *Rhacolepis*. Although there is no firm evidence to choose one interpretation in preference to the other, the second is chosen here because it is compatible with possibilities of infraorbital fusion documented by Nelson (1969). The uppermost element is thus interpreted as representing only the dermosphenotic (Fig. 6, Dsp). The additional sensory canal branch is therefore regarded as a supernumerary branch (see p. 186); the pattern of branching is somewhat similar in the dermosphenotic of *Rhacolepis*.

Dunkle (1940: fig. 9) shows a very small dermosphenotic separate from a larger infraorbital. I have regarded both as being the dermosphenotic. It is possible that the dermosphenotic ossifies from two centres in some individuals. This is known to happen in *Brycon meeki* (Weitzman 1962). However, it is also possible that the suture shown by Dunkle is, in fact, a breakage since the uppermost posterior infraorbital is strongly curved inward anterodorsally. The dermosphenotic, as reconstructed here, is comparable with the dermosphenotic of *Rhacolepis* and *Pachyrhizodus megalops*.

Opercular series. The opercular bones are shown in Fig. 6. In proportion they are different from those illustrated by Dunkle (1940: fig. 9), who indicates the posterior margins by dashed lines implying a degree of uncertainty. The large curvature shown in the transverse vertical plane of the operculum is noteworthy. In some specimens the operculum is broken along a line running back from the level of the hyomandibular/operculum articulation. Woodward (1901: 27) suggests that the operculum is subdivided, but I would agree with Jordan & Branner (1908: 17) that this 'subdivision' is a line of frequent breakage.

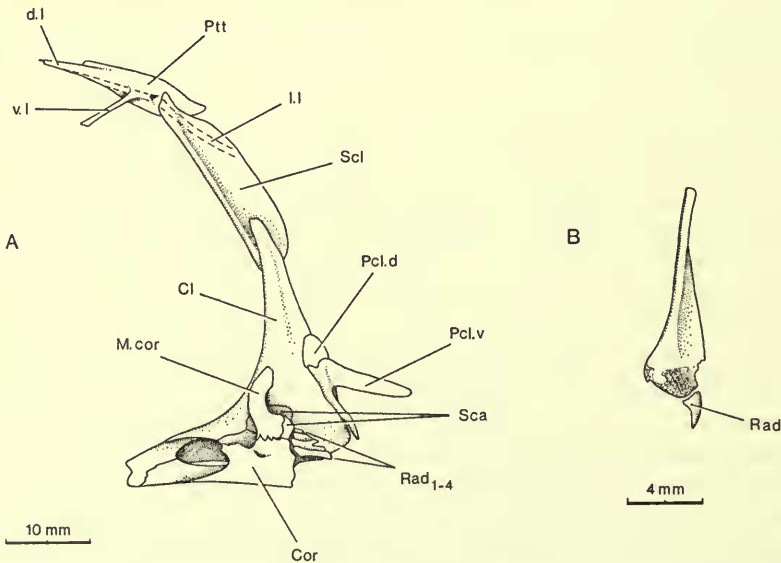


FIG. 7. *Notelops brama* (Agassiz). A: Restoration of right pectoral girdle in medial view. B: Pelvic bone and innermost radial of left side in dorsal view. Camera lucida drawing of UA 12021.

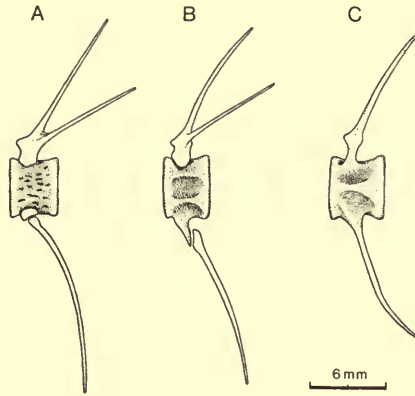


FIG. 8. *Notelops brama* (Agassiz). Vertebrae in left lateral view: A, from anterior abdominal region; B, from posterior abdominal region; C, from mid-caudal region.

Pectoral girdle and fin. The supratemporal (Fig. 6, Stt) is large and carries the supratemporal commissure. The post-temporal (Fig. 7A, Ptt) is produced to a stout dorsal or epiotic limb (Fig. 7A, d.l) and a narrow ventral or intercalar limb. The supracleithrum (Fig. 7A, Scl) is thickened along the anterior edge and this thickening is produced dorsally to a small process which fits into a depression on the underside of the post-temporal. The lateral line ran through the lateral margin of the post-temporal and obliquely through the upper portion of the supracleithrum.

The cleithrum (Fig. 7A, Cl) is the largest element of the girdle and is suturally united with the coracoid (Fig. 7A, Cor) anteriorly and posteriorly, leaving a large interosseus foramen (terminology of Starks 1930). The scapula (Fig. 7A, Sca) completely encloses the scapular foramen and the mesocoracoid (Fig. 7A, M.cor) is well developed forming the so-called 'mesocoracoid arch'. There are four proximal radials, two articulating with the scapula, two with the coracoid.

At least two postcleithra (Fig. 7A, Pcl) were seen. The dorsal postcleithrum is 'scale-like' and only slightly larger than the scales. The ventral postcleithrum is large and topographically divisible into two regions; a stout, ventrally directed rod and a thin, posteriorly directed lamina which resembles an axillary scale.

The pectoral fin (Fig. 9) is held almost horizontally and is composed of 15-17 rays. The outermost ray articulates directly with the scapula and is the only unbranched ray of the series. The longest fin-ray is the outermost and is equal to the length of sixteen abdominal vertebrae.

Pelvic girdle and fin. The pelvic fin originates beneath the posterior half of the dorsal fin. The pelvic bone (Fig. 7B) of either side is triangular and thickened along the lateral and posterior (transverse) margins. The transverse thickening was capped laterally and medially by cartilage. Three pelvic radials could be identified. The inner radial (Fig. 7B, Rad) is the largest and produced posteriorly as a narrow spur.

The pelvic fin (Fig. 9) is composed of 12-13 fin-rays, the outermost the longest (equal to the length of twelve abdominal vertebrae) and the only unbranched ray.

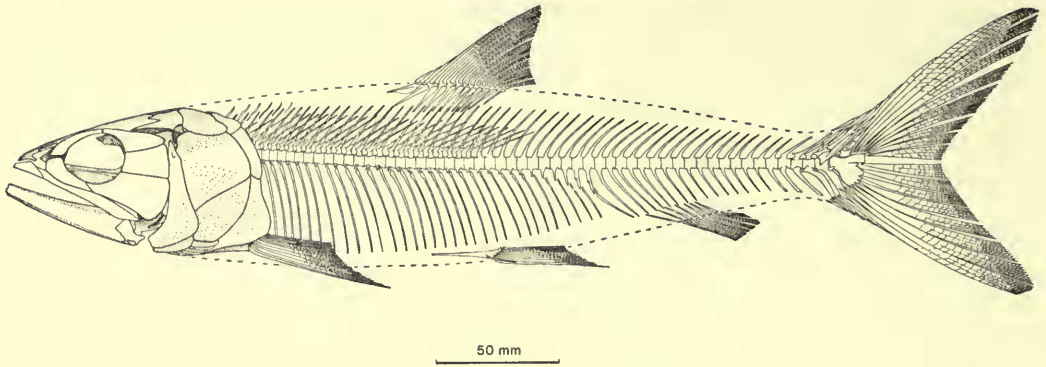


FIG. 9. *Notelops brama* (Agassiz). Entire fish, scales omitted.

Lateral to the upper half of the outermost ray there is a small, curved pelvic splint.

Vertebral column. The vertebral column is composed of approximately 60 vertebrae of which 19 or 20 are caudal. The anterior centra are deeper than long; those posteriorly are equally as long as deep. Each centrum is amphicoelous and pierced by a notochordal canal. Most of the centra are marked laterally by longitudinal ridges, but the first two or three are not ridged. The neural arches associated with the second to twenty-fifth vertebrae are autogenous. The last three neural arches and the haemal arches of Pu_{2-4} are also autogenous. The remaining neural arches, parapophyses and haemal arches are fused to the centra. The parapophyses of the last seven abdominal vertebrae increase in length with a corresponding decrease in rib length. The ribs (absent from the first centrum) are gently curved and slightly expanded proximally. The ribs do not reach the ventral midline. Short epineurals are fused with the first thirty neural arches. Several finer epineurals were seen behind this series in some specimens. No epicentral or eipleural intermusculars were seen.

The last three caudal vertebrae are modified to support the caudal fin and are described with the caudal skeleton. Approximately seven supraneurals are seen behind the occiput.

Dorsal and anal fins. The dorsal and anal fins may be seen in Fig. 9. The dorsal fin originates above the twenty-second vertebra and occupies a length of about ten vertebrae. The fin contains 15 or 16 rays supported by 12 or 13 pterygiophores; the fifth ray is the longest, being equal to the length of about thirteen vertebrae, and is the first branched ray of the series.

The anal fin is situated nearer to the caudal peduncle than to the pelvic fin. The fin originates below the forty-eighth vertebrae and is composed of eight rays. The base length of the anal fin is equal to the length of four vertebrae. The fin is slightly deeper than the base length. The third ray is the longest and the first branched ray of the series. There are seven pterygiophores.

Caudal skeleton and fin. The specimen (BM(NH) P.49084) on which this description is based is an acid-prepared specimen that is not associated with any cranial

material. However, I am confident that it belongs to *Notelops brama* since the vertebral ornamentation is similar to complete specimens of this species and it is similar (as far as comparisons can be made) to the specimen identified as *Calamopleurus cylindricus* Agassiz (= *Notelops brama*) by Jordan (1907 : pl. 2) and again by Jordan & Branner (1908 : pl. 3).

The caudal fin-rays are supported by structures associated with three preural and two ural centra. The haemal spines on Pu_{1-3} are robust and the parhypural (Fig. 10, Ph) is characteristically angled; a similarly angled parhypural is seen in *Ananogmius* and American species of *Pachyrhizodus*. The parhypural appears fused with Pu_1 . The fused condition may represent either an ontogenetic phenomenon or co-ossification. The lower hypurals form a broad plate which is fused to the first ural centrum (Fig. 10, $U_1 + H_1 + H_2$). The hypural foramen (Fig. 10, fh) in the lower hypural plate marks the proximal division between H_1 and H_2 , showing that the base of H_1 is the narrower (cf. elopiforms : Nybelin 1973, Forey 1973b). Only two upper hypurals (Fig. 10, H_3 and H_4) could be identified. H_3 and H_4 articulate with the second ural centrum. The gap in the specimen, left between H_4 and the uroneurals, suggests that more upper hypurals were present.

At least two uroneurals are present (Fig. 10, Un_{1-2}). The first is expanded proximally and covers much of the lateral face of Pu_1 ; the second is splint-like. A third uroneural may be present (Fig. 10). Articulating with Pu_1 there is a large arcual element (Fig. 10, $NaPu_1 + U_1$), which probably represents the first preural ural arch fused with the first ural neural arch. This interpretation is based on the width of

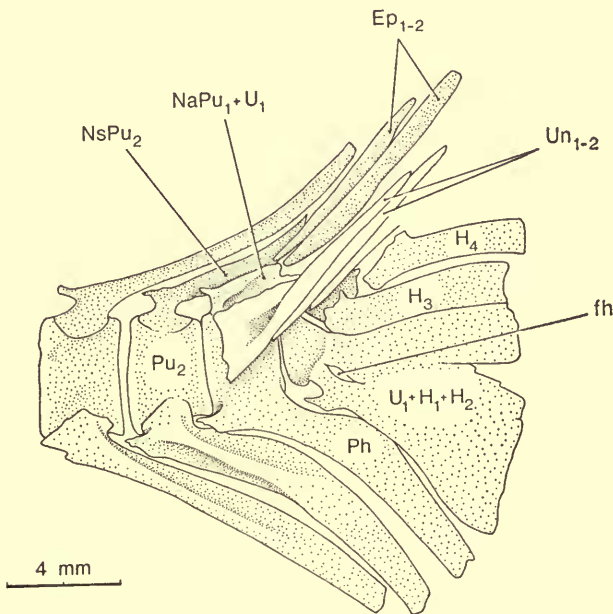


FIG. 10. *Notelops brama* (Agassiz). Caudal skeleton in left lateral view. Based on BM(NH) P.49084.

this arcual element. Pu_2 bears a neural arch and half-length neural spine (Fig. 10, $NsPu_2$). The neural spine associated with Pu_3 is full length. The neural arch elements are autogenous. There are two elongate epurals (Fig. 10, Ep_{1-2}).

The forked caudal fin contains 19 principal fin-rays. There are 9 branched principal rays in the upper lobe, 8 in the lower lobe. The inner principal fin-rays are profusely branched. The upper principal fin-rays overlies the hypural support at a steep angle. Preceding each of the outer principal fin-rays there are five procurrent rays.

Squamation. Cycloid scales are present over the body and extend onto the base of the tail. The scales are thin and circular, the focus is central and there are many evenly spaced circuli. The anterior field contains bone-cell spaces. The lateral line scales bear a small tube.

There are 90-100 scales in the lateral line series. Anterior to the caudal fin the transverse count appears to be 11 scales above the lateral line scale and 14-16 below. A large pectoral axillary scale is present.

Other species of Notelops. Jordan & Branner (1908) described a second species of *Calamopleurus* (= *Notelops*), *C. vestitus* from the Santana Formation of Ceará, Brazil. This species was said (Jordan & Branner 1908) to differ from the type species in showing larger scales and a smaller suboperculum. These authors suggested that these differences may warrant generic separation. Jordan (1921), in fact, separated *C. vestitus* from *Calamopleurus* and placed it in the genus *Brannerion* Jordan, demonstrating further points of difference from *Notelops brama*. He restudied the type specimen (No. 11, Rocha collection) of *Brannerion vestitum* (Jordan & Branner) and assigned a few other specimens to this species. According to him, *Brannerion vestitum* apparently differs from *Notelops brama* in many respects: the scales are much larger, the operculum has a convex ventral margin which is very oblique, the suboperculum is smaller, the mandible is projecting and the maxilla is short and reaches to beneath the middle of the orbit, the body is much shorter and deeper, the anal fin is long and originates beneath the dorsal fin and, if the specimen figured by Jordan (1921: pl. 4, fig. 2) is correctly referred to *Brannerion vestitum*, the ribs and haemal spines are long and nearly straight. These differences are substantial. There are no details of the cranium or the caudal skeleton well enough known to confirm (or reject) the suggestion that *Brannerion vestitum* is related to *Notelops*. It may be significant that what is known of the body form, the shapes and sizes of the opercular bones, and the general appearance of the vertebral column (only a general impression is figured by Jordan) is similar to those areas in *Hiodon*. Clearly, very much more detailed anatomy needs to be known to substantiate such a claim.

Family PACHYRHIZODONTIDAE Cope 1872

DIAGNOSIS (emended). Pachyrhizodontoid fishes in which the skull roof is broad and convex in the otic region, bone-enclosed ethmoid commissure absent, frontal margin excavated above autosphenotic spine, parietals separated by supraoccipital; subtemporal fossa absent, intercalary small, not reaching prootic, trigeminal foramen

opening directly to orbit, myodome open posteriorly, parasphenoid deep beneath otic region ; palatine short, ectopterygoid with teeth ; lower jaw with anguloarticular and retroarticular ; dentary with single row of teeth ; gular plate absent.

Genus *RHACOLEPIS* Agassiz 1841

1841 *Phacolepis* Agassiz : 83.

DIAGNOSIS (emended). Pachyrhizodontid fishes in which the skull roof is without a marked depression at the level of the autosphenotics, dermethmoid with lateral projections, dilatator fossa without a complete roof, pterotic produced to a short spine ; exoccipitals meeting above but not below foramen magnum, endochondral elements of the otic region of the braincase united by interdigitating sutures, no fenestra between autosphenotic and pterotic, lateral face of prootic with a well-developed ridge running from the posterior opening of the jugular canal to the orbital artery foramen, vomer with two recurved teeth ; ectopterygoid with short dorsal process and a single row of pointed teeth ; anterior ceratohyal fenestrated ; posterior infraorbitals overlying preoperculum ; preoperculum with truncated vertical limb and produced to a spine-like process anteroventrally, operculum with oblique ventral margin, interoperculum longer than deep ; posterior margin of cleithrum excavated opposite fin insertion ; caudal fin-rays not crossing hypurals at a steep angle ; scales small, ovoid and marked by circuli in the dorsal and ventral fields, posterior field with fine radiating ridges, focus central, scales extending over the base of the caudal, dorsal and anal fins.

TYPE SPECIES. *Rhacolepis buccalis* Agassiz.

Rhacolepis buccalis Agassiz

(Figs 11-24)

1841 *Rhacolepis buccalis* Agassiz : 83.

1844a *Rhacolepis buccalis* Agassiz : 1011.

1887 *Rhacolepis buccalis* Agassiz ; Woodward : 539 ; pl. 46, figs 2-7 ; pl. 47, figs 1-3.

1901 *Rhacolepis buccalis* Agassiz ; Woodward : 30.

1908 *Rhacolepis buccalis* Agassiz ; Jordan & Branner : 21 ; figs 12, 13 ; pl. 6, fig. 2.

1921 *Rhacolepis buccalis* Agassiz ; Jordan : 62 ; pl. 8, figs 1-5.

1968 *Rhacolepis buccalis* Agassiz ; Santos & Valença : 348, fig. 6.

DIAGNOSIS (emended). *Rhacolepis* reaching 250 mm total length ; head length equal to 22 per cent of standard length, maximum depth trunk equal to 17-19 per cent of standard length ; fin-ray counts, P. 16 or 17, V. 10 or 11 ; estimated total number of preural vertebrae 55-65 of which about 20 are caudal ; paired fins short, pelvic fin originating behind the level of the dorsal fin and situated nearer to the caudal peduncle than to the pectoral fin ; posterior infraorbitals twice as broad as deep ; diameter of orbit equal to about 20 per cent of head length ; premaxilla equal to 21 per cent of length of upper jaw, with about 10 marginal teeth ; maxilla with about 35 teeth ; dentary with about 35 teeth ; preopercular sensory canal with 8-10 ventral branches ; about 90 lateral line scales, approximately 20 scales

in transverse series anterior to dorsal fin, scales deeper than long, deeply overlapping.

HOLOTYPE. BM(NH) P.4314a, a crushed head, Santana Formation (Aptian), Ceará, Brazil.

MATERIAL. Twenty-six specimens in the British Museum (Natural History), four in the University of Alberta and one in the American Museum of Natural History were examined.

FORMATION AND LOCALITY. Santana Formation (Aptian), Ceará, Brazil.

DESCRIPTION. The species here referred to the genus *Rhacolepis* Agassiz have never been satisfactorily described. Woodward (1887) gives a composite description with *Notelops brama*, implying that the two genera are closely similar. In fact, the genera are rather different, with *Rhacolepis* being more advanced in several respects (p. 192). The following description is an account of the osteology of *Rhacolepis buccalis* (as representative of the genus), and will serve to emphasize the points of difference from the osteology of *Notelops*.

Braincase. The braincase is long and shallow, being three times as long as deep. The greatest width of the braincase occurs at the level of the autosphenotic (cf. *Notelops*) and is equal to two-thirds of the braincase length. The roofing bones of the skull are smooth, except for the ridges associated with sensory canals and

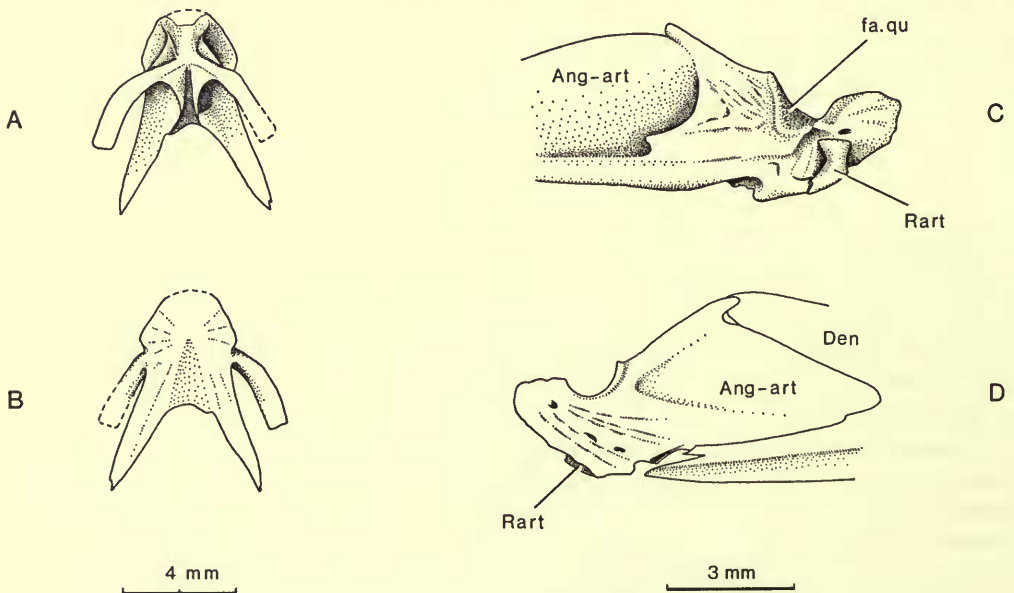


FIG. 11. *Rhacolepis buccalis* Agassiz. A: Dermethmoid in ventral view. B: Dermethmoid in dorsal view. Camera lucida drawings of isolated bone from UA 12026. C: Posterior portion of angulo-articular in medial view. Camera lucida drawing from UA 12026; retroarticular from AMNH 4617. D: Posterior portion of right mandibular ramus. Based on UA 12026 and AMNH 4617.

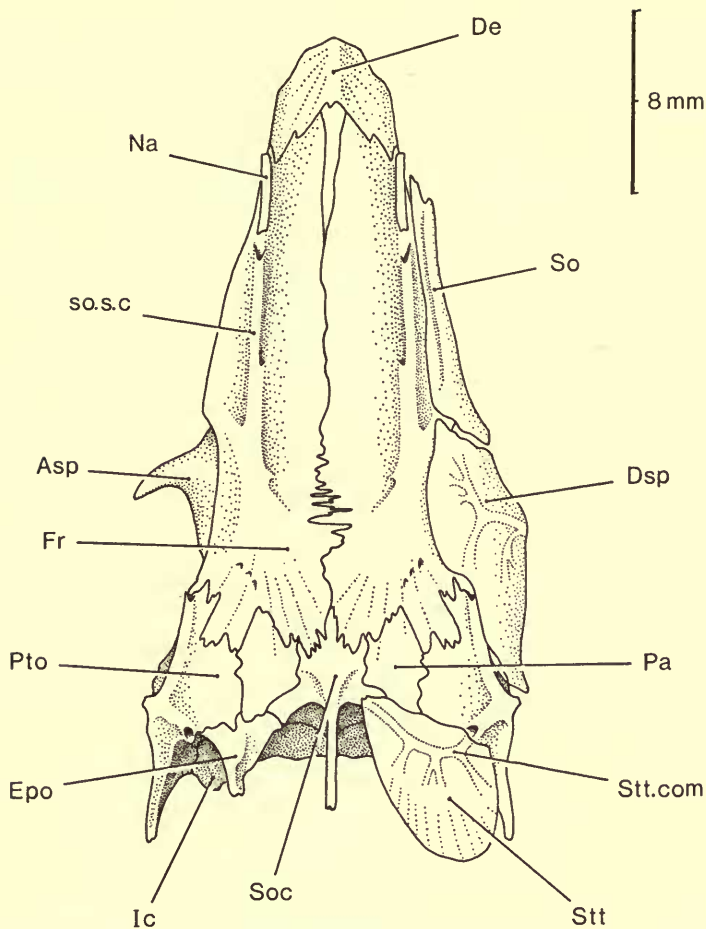


FIG. 12. *Rhacolepis buccalis* Agassiz. Restoration of skull roof. Supraorbital, dermosphenotic and supratemporal shown on right side only.

smaller radiating ridges on the dermethmoid and the posterior limits of the frontals. In unprepared specimens the dermal bones are much smoother than the corresponding elements in *Notelops*.

The dermethmoid is of complex shape. The main body of the dermethmoid (Fig. 11A, B; Fig. 12, De) forms a broad, triangular plate which overlies the anterior ends of the frontals. Ventrally (Fig. 11A), the dermethmoid bears paired ventrolateral projections which are longer than those in *Notelops*. Anterior and posterior to each lateral projection, the ventral surface is raised into 'cones', the tips of which converge at the base of the ventrolateral projections. The shape of the dermethmoid appears to change during ontogeny, the smaller (presumably younger) individuals having a narrower dermethmoid with relatively larger ventrolateral projections. The entire structure here termed the dermethmoid appears to

be composed of dermal bone; if there is a perichondral component, it is certainly not recognizable. There is no evidence that the ventrolateral projections are ontogenetically separate from the main body (cf. Weitzman 1967 on *Megalops*). The dermethmoid bears no evidence of an ethmoid commissure (cf. *Notelops*; Fig. 1, e.com).

The frontal (Fig. 12, Fr) meets its antimere over most of its length, except anteriorly where the cartilage of the ethmoid region was presumably present. The interfrontal suture becomes complex in the epiphyseal region, a point of distinction from that of *Notelops* (Fig. 1). Above the orbit the frontal is raised in the mid-line so that together the frontals form a median ridge (see also Woodward 1887: pl. 46, fig. 3). Such a ridge is not seen in *Notelops*. The supraorbital sensory canal (Fig. 12, so.s.c) opens medially above the epiphyseal region and at the mid-orbital level. Anteriorly the canal opens onto the surface of the frontal. The sensory canal continued forward in a small, tubular nasal (Fig. 12, Na). The posterior branches of the supraorbital sensory canal could not be accurately determined. Three small pores are generally seen (Fig. 12) but there is no major branch suggesting a linkage between supraorbital and infraorbital sensory canals. On the basis of several suitably prepared specimens, I conclude that there was no supraorbital-infraorbital canal connection. The lateral margin of the frontal is excavated above the autosphenotic spine, as in the English species of *Pachyrhizodus*. This results in a partially unroofed dilatator fossa. In *Notelops* the frontal margin is not excavated and the dilatator fossa is roofed. Posteriorly the margin of the frontal is more irregular than in *Notelops*.

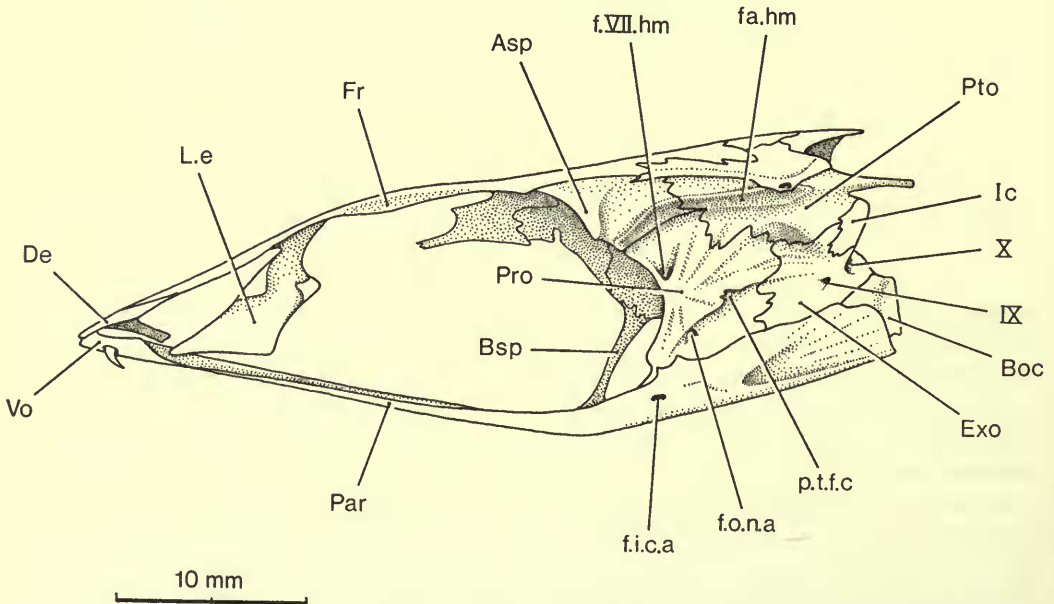


FIG. 13. *Rhacolepis buccalis* Agassiz. Braincase in left lateral view. Based on BM(NH) P.49084.

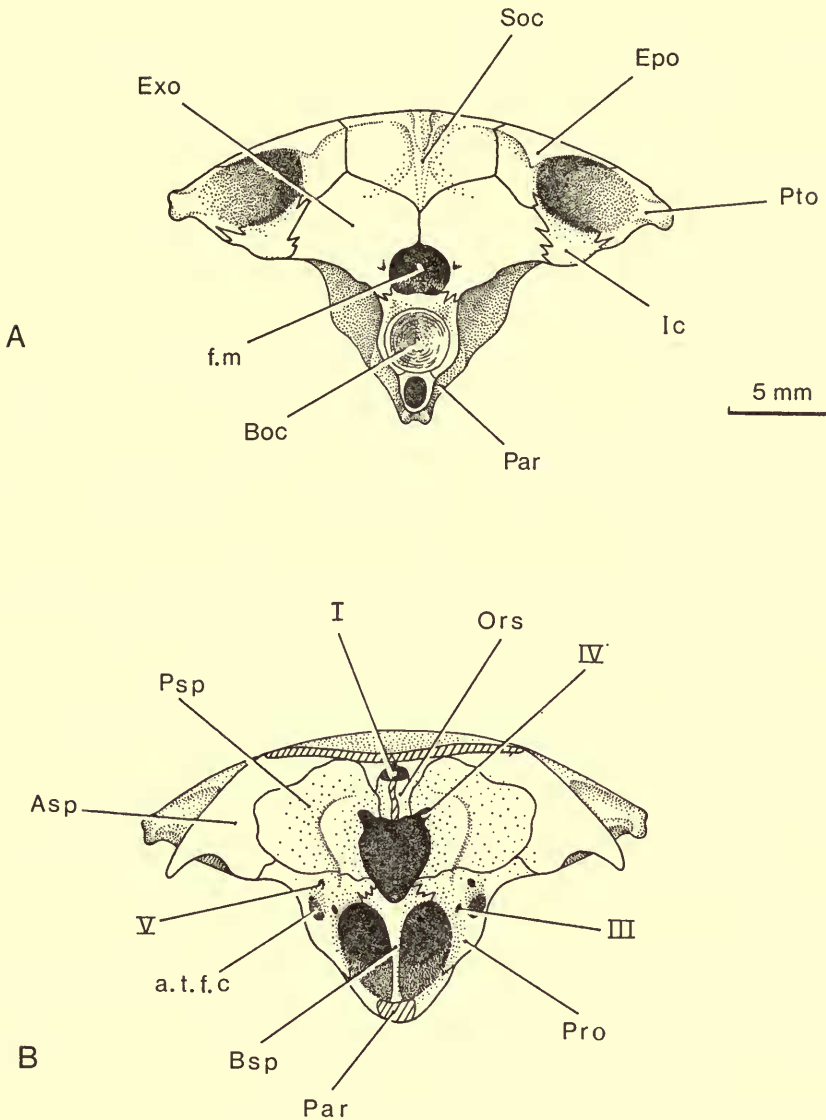


FIG. 14. *Rhacolepis buccalis* Agassiz. A: Braincase in posterior view. B: Orbital view of the postorbital part of the braincase. Both based on BM(NH) P.49084.

The pterotic (Figs 12, 13, 14A, Pto) constitutes a smaller proportion of the skull-roof area than in *Notelops*. Posteriorly the pterotic is produced as a prominent spine, absent in *Notelops*. The temporal sensory canal runs at the lateral margin of the pterotic and opens laterally to receive the preopercular sensory canal. From here the temporal canal runs posteromedially to open above the post-temporal fossa. In *Notelops* (Fig. 1) it may be seen that the temporal canal runs away from the lateral margin of the pterotic, leaving a small 'ledge' of bone overlying the dilatator

fossa. Topographically, this is missing in *Rhacolepis* and the posterior area of the dilatator fossa is unroofed. The lateral wall of the pterotic composes the posterior halves of the dilatator fossa and the hyomandibular facet (Figs 13, 15, fa.hm). The parietals (Fig. 12, Pa) are small, irregular, and are separated by the supraoccipital. The separated parietals of *Rhacolepis* are contrasted with the medially united condition in *Notelops*.

The supraoccipital (Figs 12, 14A, Soc) bears a well-developed spine which continues forward as a ridge upon the main body of the bone. The epiotic (Figs 12, 14A, Epo) is produced as a well-developed process which bears a ridge receiving the epiotic (dorsal) limb of the post-temporal.

The exoccipital (Figs 13, 14A, Exo) is pierced by foramina for the vagus and glossopharyngeal nerves, as in *Notelops*. In *Rhacolepis* these foramina are closer together than in *Notelops*. The intercalar (Figs 13, 14A, Ic) is less complex than in *Notelops*, and there is no prootic-intercalar bridge. In *Rhacolepis* the intercalar is smooth and interdigitates with the exoccipital, pterotic and epiotic. In posterior view (Fig. 14A) the intercalar may be seen to form the ventral margin of the opening to the post-temporal fossa.

The basioccipital (Figs 13, 14A, Boc) forms the occipital condyle and the ventral margin of the foramen magnum. In *Notelops* the exoccipitals meet below the foramen magnum (Dunkle 1940: fig. 1B). Immediately behind the foramen magnum the dorsal surface of the basioccipital is marked by a pair of pits (UA 12026), presumably for the reception of neural arches - these latter elements were not seen. The presence of the pits suggests that a centrum element has been incorporated into the basioccipital of *Rhacolepis*. A similar situation exists in *Pachyrhizodus megalops*. Pits are not present on the basioccipital of *Notelops*, although it is still possible that the basioccipital contains a centrum element. In lateral view (Fig. 13) the basioccipital does not appear to be as large as in *Notelops* (Fig. 2), but this is because the parasphenoid of *Rhacolepis* has a broad overlap with the basioccipital.

The prootic (Figs 13, 14B, 15, Pro) is, as usual, a large element. Laterally, the prootic meets the pterotic, exoccipital and basioccipital in an interdigitating suture; a point of distinction from the corresponding sutures of *Notelops* (Fig. 2 and Dunkle 1940: fig. 1C). As in *Notelops*, the lateral face of the prootic is pierced by three foramina, each leading into the jugular canal. Dorsally, there is a large foramen for the exit of the hyomandibular trunk of the facial (Figs 13, 15, f.VII.hm); ventrally there is a foramen for the entry of the orbital artery (Fig. 13, f.o.n.a); posteriorly there is a foramen for the exit of the jugular (head) vein (Fig. 13, p.t.f.c). The posterior palatine branch of the facial descended through the prootic bridge into the myodome, and then pierced the lateral wall of the myodome (formed by the prootic) at the level of the foramen for the orbital artery. Therefore, in lateral view, the foramen for the orbital artery also opens to the myodome. In *Rhacolepis* there is a ridge on the lateral face of the prootic, running from above the foramen for the head vein anteroventrally to above the foramen for the orbital artery. Presumably this ridge served as a site of attachment for part of the superficial branchial musculature: such a ridge is not present in *Notelops*. There is no

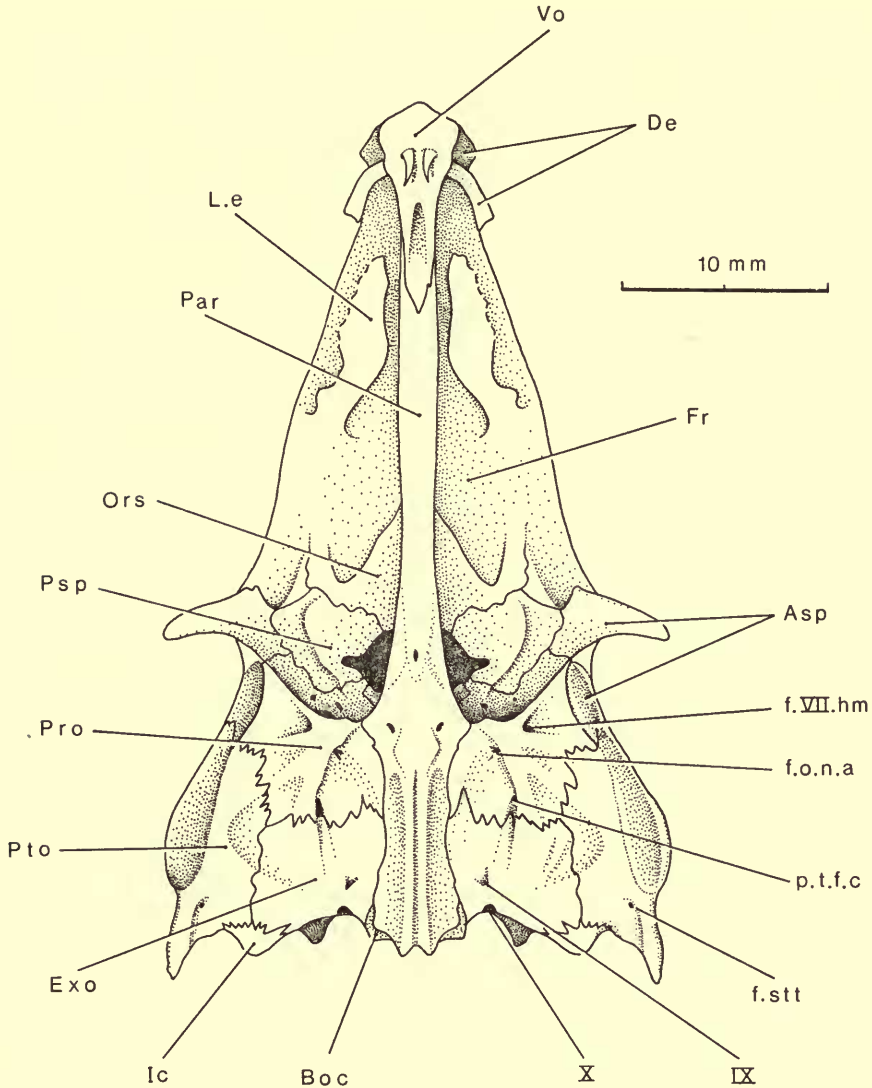


FIG. 15. *Rhacolepis buccalis* Agassiz. Braincase in ventral view. Based on BM(NH) P.49084.

well-defined subtemporal fossa in *Rhacolepis* (cf. *Notelops*), only a broad, shallow depression remains (see p. 194 for a possible functional explanation).

The anterior, orbital face of the prootic (Fig. 14B, Pro) is pierced by three foramina. Laterally, there is a foramen (Fig. 14B, a.t.f.c) for the jugular vein, orbital artery and the buccal and superficial ophthalmic branches of the facial. Dorsal to this large foramen is a smaller foramen (Fig. 14B, V) for the trigeminal nerve. In *Notelops* both the anteriorly running branches of the facial and the trigeminal run

into the jugular canal before passing into the orbit. It appears that in *Rhacolepis* the prefacial commissure, separating the facial from the trigeminal foramina, is so wide as to 'displace' the trigeminal foramen anteriorly, beyond the limits of the lateral commissure. It is of interest to note that *Pachyrrhizodus megalops* is similar to *Rhacolepis* in this respect (p. 167). A third foramen, the oculomotor foramen (Fig. 14B, III), lies medial to the anterior opening of the jugular canal. The profundus nerve ran through the trigeminal foramen, or in a few individuals examined through a separate foramen situated very near the trigeminal foramen. The abducens ran through the prootic bridge, as in *Notelops*.

The autosphenotic (Figs 12, 13, 14B, 15, Asp) is produced as a prominent spine and also forms the anterior half of the facet for the hyomandibular. There is no fenestra between the autosphenotic and pterotic as there is in *Notelops* (Fig. 2). Similarly there is no large foramen in the orbital face of the autosphenotic as there is in *Notelops* (p. 133). A foramen for the otic branch of the facial could not be identified.

The pterosphenoid (Figs 14B, 15, Psp) is large and is marked by a prominent crest which runs up and forward. The superficial ophthalmic branches of the facial and trigeminal ran along the lateral edge of this crest. The pterosphenoid forms much of the lateral margin of the optic foramen and, as may be seen in Fig. 14B, a deep notch in the margin shows where the trochlear (IV) left the endocranial cavity.

The orbitosphenoid (Ors) and basisphenoid (Bsp) are unremarkable; the shapes, relative sizes and position may be seen in Figs 13, 14B and 15.

The lateral ethmoid (Figs 13, 15, L.e) is thin and appears to be formed entirely by perichondral bone, a point of distinction from the lateral ethmoid (parethmoid of Dunkle 1940: 172) of *Notelops*, in which there is a thin layer of endochondral bone lining perichondral bone. The lateral ethmoid of *Rhacolepis* spreads anteroventrally as a broad sheet, ending beneath the ventrolateral projections of the dermethmoid.

The vomer (Fig. 15, Vo) is expanded anteriorly, where it meets the dermethmoid. Posteriorly, the vomer passes into a grooved lamina which underlies the anterior end of the parasphenoid. The vomer bears two pointed teeth (Fig. 15) set into sockets in the head of the bone. The teeth are larger than those borne by the dermal jaw bones and are recurved. Between the vomer, dermethmoid and lateral ethmoids there is a space, suggesting that the internasal septum and nasal capsules were cartilaginous.

The parasphenoid (Figs 13, 14, 15, Par) is long, narrow beneath the orbit and deep beneath the otic region. There is a marked angle in the parasphenoid at the basisphenoid insertion. At this point the parasphenoid is pierced by an oblique median canal, the buccohypophyseal canal. The foramen for the internal carotid artery (Fig. 13, f.i.c.a) occurs beneath the poorly-developed ascending wing. Immediately posterior to this foramen is a low prominence which is the point of articulation for the first infrapharyngobranchial. The posterior part of the parasphenoid is marked by a mid-ventral groove and broader lateral grooves. Posteriorly, the ventral surface of the parasphenoid does not meet the basioccipital resulting in the myodome being open posteriorly. This opening may be seen in Fig. 14A; such a foramen is not present in *Notelops*.

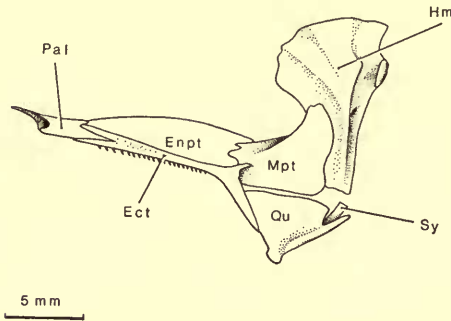


FIG. 16. *Rhacolepis buccalis* Agassiz. Restoration of the left hyopalatine series in lateral view.

Hyopalatine series. The hyomandibular (Fig. 16, Hm) has a broad head and a moderately wide shaft that is held vertically. A ridge runs on the outer face of the shaft but is not as well developed as it is in *Notelops*.

The metapterygoid (Fig. 16, Mpt) bears a well-defined ridge which divides the bone into an inner horizontal and an outer vertical portion. The latter overlaps a thin lamina of the hyomandibular. The quadrate (Fig. 16, Qu) has the shape of an equilateral triangle and is thus different from that of *Notelops* (Fig. 3). The dorsal margin is only weakly emarginated for the reception of the symplectic (Fig. 16, Sy). The endopterygoid (Fig. 16, Enpt) is similar to that in *Notelops* and bears a similar dentition of many fine granular teeth (Fig. 18).

The ectopterygoid (Fig. 16, Ect) is narrow and produced as a dorsal process just above the metapterygoid. Unlike that of *Notelops*, the ectopterygoid bears a single row of approximately 20 small, recurved teeth, and thus forms a functional part of the oral surface of the palate. The palatine (Fig. 16, Pal) is small (cf. *Notelops*, Fig. 3) and is represented by a dorsoventrally flattened tube of bone. Anteriorly the 'tube' is open anterolaterally; posteriorly the opening is filled by the ectopterygoid and the endopterygoid. There are no teeth on the palatine. The terminology of the element here called the palatine is in doubt. The element clearly represents at least the autopalatine of a teleostean fish such as *Tarpon*. There is no separate dermopalatine, but neither is there evidence of fusion between an autopalatine and an edentulous dermopalatine or evidence of loss of the dermopalatine. The palatine of *Notelops* represents the result of fusion between autopalatine and dermopalatine elements.

Dermal upper jaw. The upper jaw reaches back to the hind margin of the orbit and is composed of the premaxilla, maxilla and a single supramaxilla. The premaxilla (Fig. 17A, B) is equal to one-fifth of the total jaw length, and is almost as deep as long. The premaxilla consists of a stout lower portion with a thin semi-circular wing which projects dorsally and abuts onto the dermethmoid. Anteriorly and dorsally the premaxilla shows an external convexity. In medial view (Fig. 17A) a V-shaped groove is seen posteriorly and a deep pocket, which is open dorsally, may be seen anteriorly. A premaxilla-ethmoid ligament may well have been

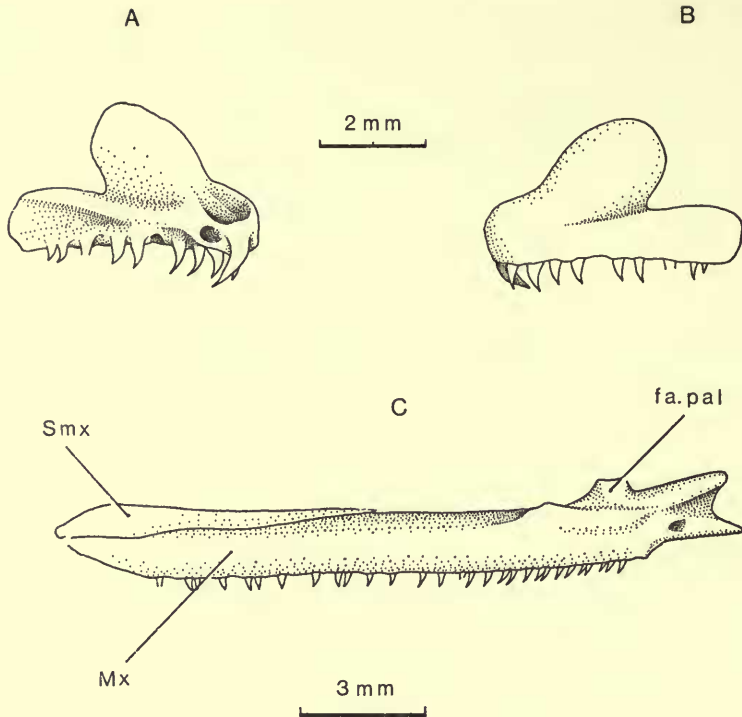


FIG. 17. *Rhacolepis buccalis* Agassiz. A: Left premaxilla in medial view. B: Left premaxilla in lateral view. Camera lucida drawings of isolated bone from UA 12026. C: Right maxilla and supramaxilla in lateral view.

inserted into this pocket. There are 10 marginal teeth, each distally recurved, the bases of which appear to be fused with the supporting bone. Additionally, there is one inner tooth at the anterior end of the premaxilla. It is considerably larger than a marginal tooth and is inclined almost horizontally. In most specimens examined there is a socket behind the inner tooth (Fig. 17A).

The maxilla (Fig. 17C, Mx) is elongate, with the head produced as two prongs joined by a bridge of thin bone. The ventral prong fits into the V-shaped groove of the premaxilla, making it unlikely that the premaxilla moved independently of the maxilla. A small, posteriorly directed fossa is present at the base of the ventral prong. This may have contained a ligament. There is no special facet developed for articulation with the ethmoid. The facet for articulation with the palatine (Fig. 17C, fa.pal) is well developed, and immediately behind this there is a low crest which may represent the point of insertion for a palatomaxillary ligament. There are approximately 35 teeth set in a single row on the maxilla. The teeth are slightly recurved and the bases appear fused with the supporting bone. A narrow ledge of bone lies lateral to the tooth base, thus in lateral view the true length of the tooth is not seen. In UA 12026 a maxilla 20 mm in length bears teeth 0.6 mm long. The

supramaxilla (Fig. 17C, Smx) is represented by a thin splint half as long as the maxilla.

The lower jaw. The mandibular ramus is slightly longer than the upper jaw ; it is generally shallow with a poorly-developed coronoid process. It differs from the lower jaw of *Notelops* in the fusion of elements posteriorly and in the dentition.

The dentary (Figs 11D, 19, Den) forms the major component of the mandibular ramus and overlaps the angulo-articular except at the coronoid process where the latter overlaps the former, a condition similar to that seen in *Notelops*. The lower margin of the dentary is slightly inflected. The dentary bears a single row of approximately 35 teeth, each of which is the same shape, but slightly larger than a maxillary tooth.

The angular and articular have fused together forming an angulo-articular (Fig. 11C, D, Ang-art). The articular portion, recognizable as a more 'spongy' ossification, appears to form most of the articulatory facet (Fig. 11C, fa.qu). A well-developed postarticular process is present behind the articulatory facet. The posteroventral aspect of the angulo-articular is ornamented with ridges (Figs 11D, 19). The retroarticular (Figs 11C, 19, Rart) is a small 'hourglass-shaped' element loosely connected to the inner surface of the angulo-articular, ventral and slightly posterior to the articulatory facet. It is often dissociated in acid-prepared specimens.

The mandibular sensory canal runs through the angulo-articular and the dentary. The canal opens to the lateral surface of the angulo-articular by three pores. In the dentary there are seven or eight short branches, each of which opens via a terminal pore. On the medial surface of the angulo-articular there is an anteriorly directed pore (seen in Fig. 11C) but it is uncertain if this led to the mandibular sensory canal.

Hyoïd bar, urohyal, branchiostegal rays and gill arches. The ceratohyal is, as usual in lower teleosts, ossified in two sections representing anterior and posterior ceratohyals (Figs 18, 19, Ce.a, Ce.p), which were no doubt connected to one another by a cartilage-filled suture. The anterior ceratohyal is fenestrated and bears a deep lateral groove, and the posterior ceratohyal is grooved and sometimes fenestrated (Fig. 18). At the posterior end of the groove on the posterior ceratohyal there is a deeper pit which marks the point of origin of the hyoidean-mandibular ligament. There are two well-ossified hypohyals, the dorsal hypohyal slightly larger than the ventral. The interhyal is a small rod-like bone (Fig. 19, Int).

The exact number of branchiostegal rays is not known. Woodward (1887) records a count of twenty and this is probably a realistic estimate. There are approximately eight blade-like branchiostegal rays attached to the posterior ceratohyal. The anterior ceratohyal carries a series of approximately twelve fine rays which, as Woodward (1887) noted, are rather widely spaced.

The urohyal (Fig. 18, Ur) is long. Anteriorly it is rod-like. A cross-section through the posterior end would display an inverted V-shape with the tips of the limbs thickened.

The gill arches are reasonably well known from AMNH 4617, UA 12026 and particularly UA 12028 (Fig. 18). Most of the endochondral elements are ossified

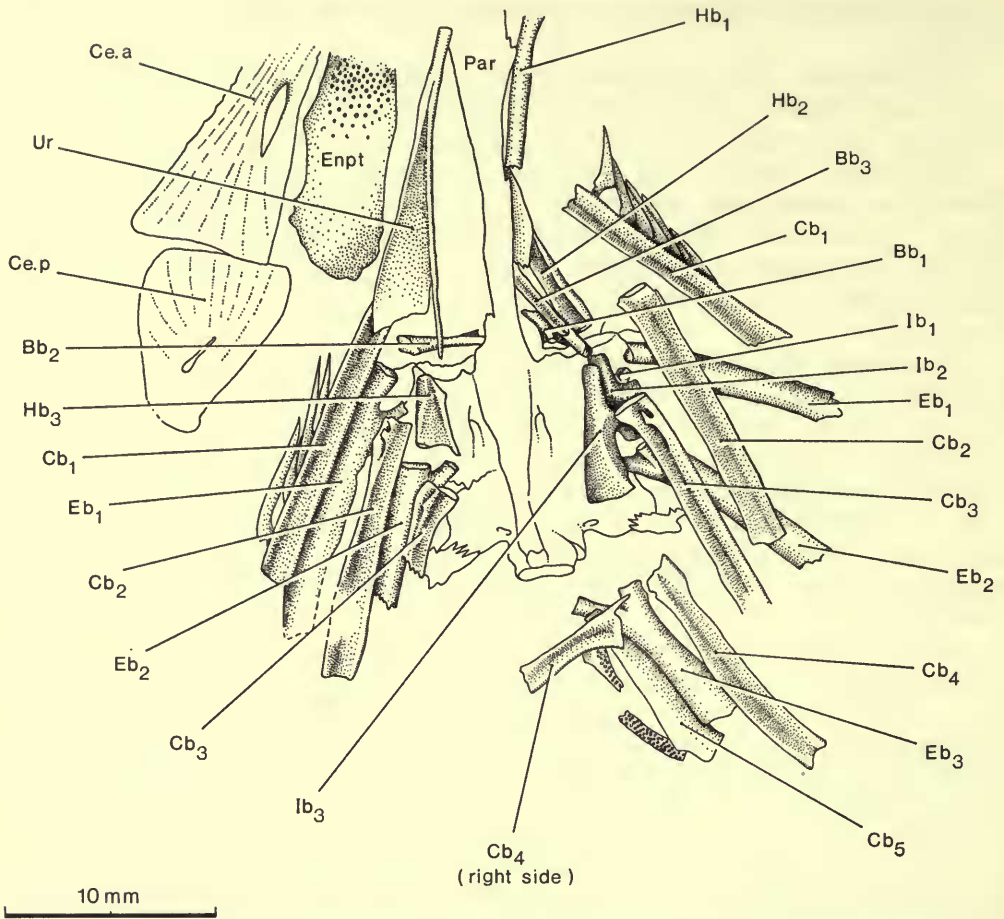


FIG. 18. *Rhacolepis buccalis* Agassiz. Camera lucida drawing of UA 12028 showing gill arches, braincase (in outline) and associated structures in ventral view.

and the membrane elements are separate from the endochondral elements over much of the series. The first, second and third basibranchials ($Bb_{1,2,3}$) are ossified and support an elongate tooth plate (seen in AMNH 4617; Fig. 19, $Bb.tp_{1+2+3}$) which represents a fusion of tooth plates associated with the first three basibranchials. In UA 12026 there is the suggestion that the tooth plate is fused with the third basibranchial but this could not be confirmed in any other specimen. No ossified basihyal or basihyal tooth plate could be identified. It is possible that the basibranchial tooth plate referred to above also incorporates a basihyal tooth plate since it is slightly longer than the combined length of the basibranchials.

The hypobranchials may be seen in Fig. 18; as usual in teleosts the first is the longest and the third is rather short and broader than the first two. The five ceratotrichia are unremarkable. There are four ossified epibranchials (Eb);

the fourth (not shown in figure) is deeply notched for the fourth efferent branchial artery. It may be noted that the dorsal ends of the first three epibranchials are more deeply forked than in *Elops*, but the significance of this difference is not clear to the author. The first infrapharyngobranchial (Ib_1) is a small element and articulates with the braincase immediately behind the foramen for the carotid artery. The second and third infrapharyngobranchials ($Ib_{2,3}$) are larger and each bears a prominent process for articulation with the anterior epibranchial. In all, the second and third infrapharyngobranchials of *Rhacolepis* resemble those figured by Nelson (1968b : fig. 6B) for *Alepocephalus macropterus* more nearly than they do those of *Elops*.

The basibranchial tooth plate, described above, bears many small recurved teeth. Small, tooth-bearing plates are associated with the hypobranchials, ceratobranchials and epibranchials of the first two arches but their number and distribution could not

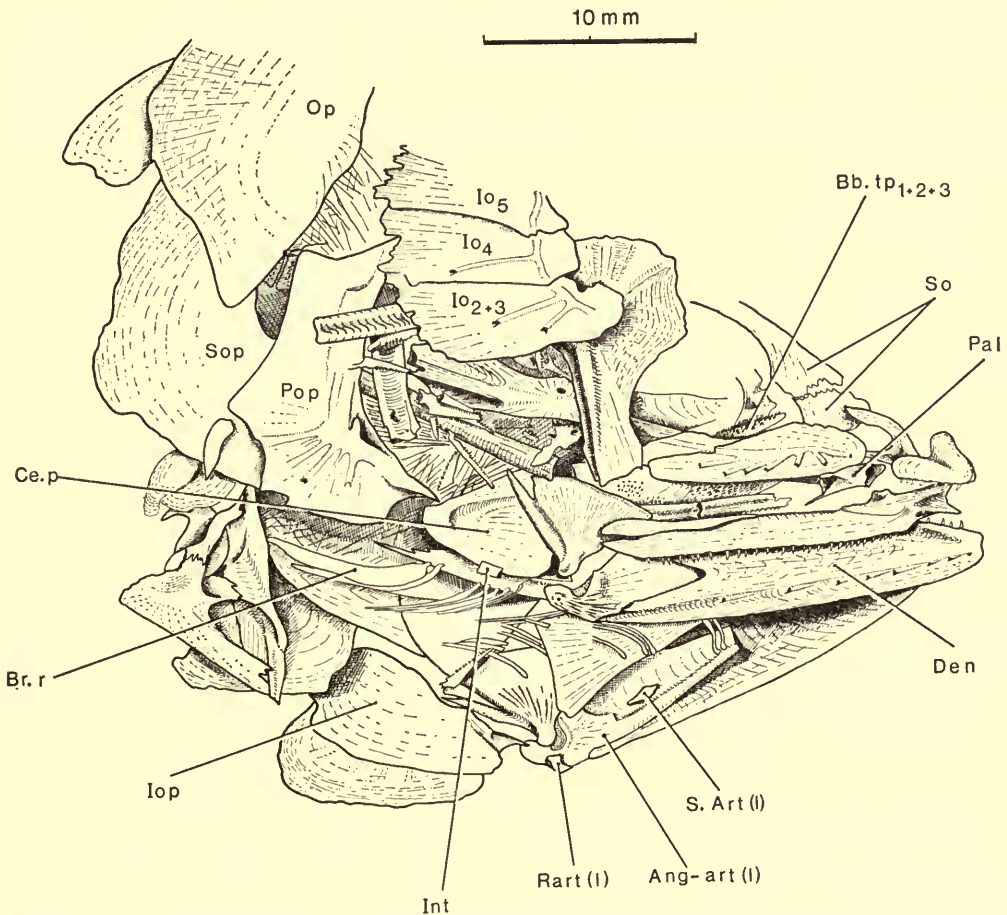


FIG. 19. *Rhacolepis buccalis* Agassiz. Camera lucida drawing of AMNH 4617.

be identified. The third epibranchial and the fifth ceratobranchial are also known to bear tooth plates. Upper pharyngeals could not be seen, but it is known (from UA 12028) that tooth plates are not fused with the second or third infrapharyngobranchials. Gill-rakers are present on the hypobranchials, ceratobranchials and epibranchials of the first two arches. They are quite long and bear many small teeth; their size and shape may be seen in Fig. 18. It is difficult to evaluate the information on the gill arch structure of *Rhacolepis buccalis*. In general terms the structure appears to be that expected in a primitive teleostean fish; most of the elements are present (a basihyal and suprpharyngobranchials were not seen), the tooth plates appear to be separate from the endochondral supports (with the possible exceptions noted) and there are no obviously specialized features. Furthermore, the gill arches cannot, at present, be compared to those of *Notelops* or *Pachyrhizodus* since the two latter are poorly known in this respect. The gill arches of *Rhacolepis buccalis* do not indicate any particular teleostean relationship.

Circumorbital series. The circumorbital series (Fig. 20) is composed of a supraorbital and five canal-bearing bones. The supraorbital (So) is narrow posteriorly where it is sutured with the dermosphenotic. It becomes broad anteroventrally where it abuts on the first infraorbital (Io₁). This latter element is elongate and rounded anteriorly, and meets the compound infraorbital behind in an oblique

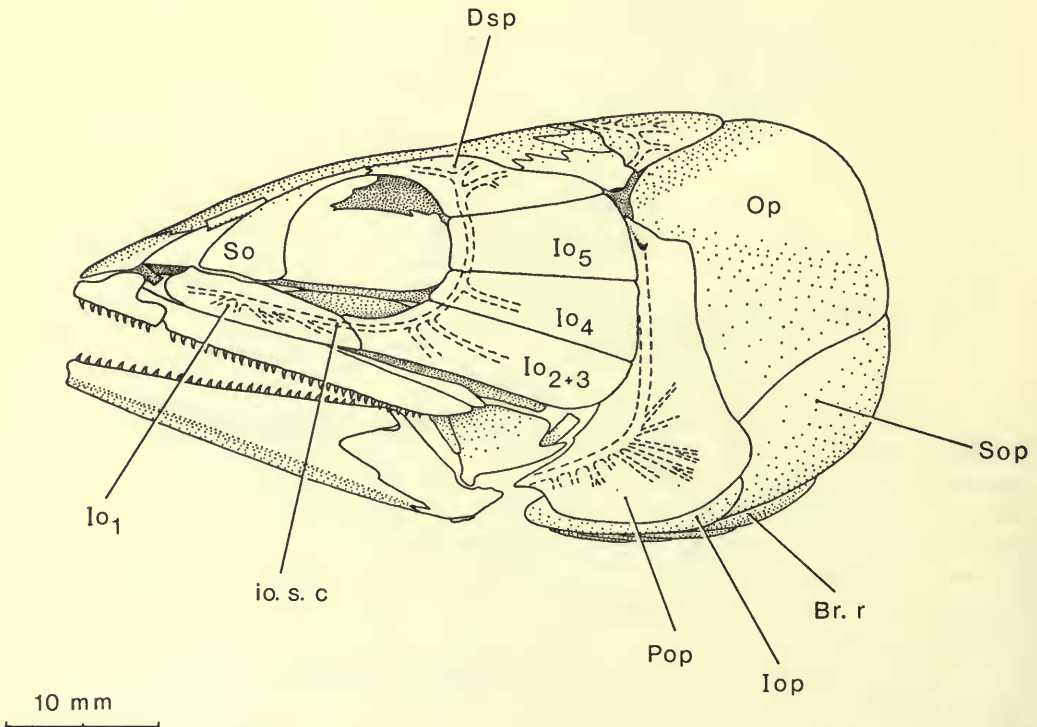


FIG. 20. *Rhacolepis buccalis* Agassiz. Restoration of cranium in left lateral view.

suture. The large infraorbital (Io_{2+3}) forming the posteroventral border to the orbit appears to represent the fused second and third infraorbitals of a primitive teleostean fish such as *Elops* (Nelson 1969). In this respect there is a resemblance to *Notelops*, but in that genus the infraorbital under discussion is deeper and carries three branches of the infraorbital sensory canal. The fourth (Io_4) and fifth (Io_5) infraorbitals are unfused (cf. *Notelops*); each is shallow but broad. The dermosphenotic (Dsp) or sixth infraorbital is large and completely covers the dilatator fossa as in *Pachyrhizodus megalops*. The dorsal margin of the dermosphenotic is contoured to fit the skull roof.

The infraorbital sensory canal (io.s.c) runs through the infraorbitals near the orbital margin. Five branches are given off in the first infraorbital, two in Io_{2+3} and one in the fourth infraorbital. Within the dermosphenotic the sensory canal splits into three branches, anterior, dorsal and posterior. The anterior branch is short but whether it opens terminally could not be ascertained. The posterior branch runs towards the frontal-pterotic contact and often bears a few ventral branches. There does not appear to be a connection between supraorbital and infraorbital sensory canals.

Opercular series. The opercular series is seen in Fig. 20. As in *Notelops* the operculum (Op) is large and dorsally is medially curved. The ventral margin is oblique and slightly concave. The suboperculum (Sop) is also relatively large. The preoperculum (Pop) differs from that of *Notelops* in being broader throughout and in having a better-developed ventral limb. The larger ventral limb in *Rhacolepis* may be due to the slightly more anterior position of the jaw articulation. Characteristically, the anteroventral margin of the preoperculum is excavated. The preopercular sensory canal runs away from the anterior margin at the base of the angle. The canal gives off approximately ten posterior/ventral branches, some of which may bifurcate. The interoperculum (Io) is broader (longer) than that element in *Notelops*.

Pectoral girdle and fin. The supratemporal (Fig. 12, Stt) is large and semicircular, as in *Notelops*. The supratemporal does not meet its partner in the midline, and if the supratemporal commissure was complete it must have run in the skin above the supraoccipital. The supratemporal commissure gives off three posterior branches within the supratemporal.

The post-temporal (Fig. 21A, Ptt) is relatively larger than that of *Notelops*, although of similar shape. The lateral line canal runs near the lateral margin. The supracleithrum (Fig. 21A, Scl) has a convex posterior margin and carries the continuation of the lateral line. There are several small posterior branches of the lateral line within the supracleithrum. The lateral line enters and leaves the supracleithrum lower down than in *Notelops*.

The cleithrum (Fig. 21A, Cl) is narrow and the dorsal limb is not as well developed as in *Notelops*. The posterior margin of the cleithrum is excavated at the fin insertion so that, in lateral view, part of the scapula and much of the coracoid may be seen. The cleithrum of *Notelops* is expanded at this level, covering both the scapula and fin insertion (Fig. 9). The scapula (Fig. 21A, Sca) completely encloses the scapular foramen and is produced posteriorly as a peg-like process. Both the

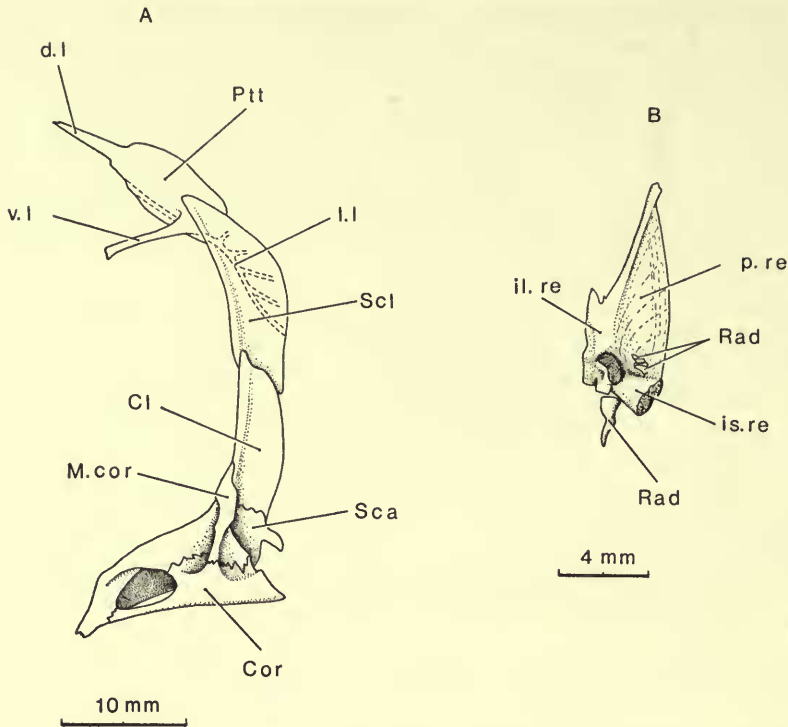


FIG. 21. *Rhacolepis buccalis* Agassiz. A: Restoration of right pectoral girdle in medial view. B: Left pelvic bone and radials in dorsal view. Camera lucida drawing of UA 12026.

mesocoracoid (Fig. 21A, M.cor) and the coracoid (Fig. 21A, Cor) are well developed. Between the cleithrum and the coracoid there is a large interosseus foramen. There are four proximal radials. The outermost is the shortest and has three articulating heads distally. The two outer radials articulate with the scapula, the inner two with the coracoid. The postcleithra are poorly known but there is sufficient evidence to suggest a similarity with those of *Notelops*.

The pectoral fin is held vertically and is composed of 16-17 rays. The outermost ray is unbranched and the second is the longest of the series, being equal in length to nine abdominal vertebrae. The fin is relatively much shorter than that of *Notelops*.

Pelvic girdle and fin. The pelvic fin originates behind the dorsal fin and is nearer to the caudal peduncle than to the pectoral fin. The fin is supported by a pelvic bone (Fig. 21B) which is more complex in shape than that of *Notelops*. The pelvic bone is thickened along the lateral and posterior margins. Between these thickenings there is a thin wing which is concave dorsally. The ischial region* is particularly

* The tetrapod adjectives ischial, pubic and iliac are useful in descriptive morphology of the teleost pelvic girdle, but the usage is not meant to imply homology with those elements in the tetrapod girdle. This practice follows Weitzman (1967).

thick and was presumably capped medially by cartilage. The iliac region bears two small articular facets along the posterior margin and a large articular facet dorsally and ventrally. Each of these facets was probably capped with cartilage. The large articular facets on the dorsal and ventral surface received the bases of the outermost one or two rays. The two posterior facets articulated with two small proximal radials. The third, innermost proximal radial is large and is produced as a spinous process but is not fused to any fin-ray. The iliac region bears a small anterior process that is separate from the main thickening in the pubic region. The pelvic bone thus shows a degree of anterior bifurcation but this is not as well developed as it is in cyprinoids or siluroids.

There are 10-11 pelvic fin-rays, the outermost the only unbranched member of the series. The fin is very short, the longest fin-ray (the outermost) being equal to the length of four caudal vertebrae. A pelvic splint bone was not seen.

Vertebral column. The exact number of vertebrae is unknown. Woodward (1887) states that there are approximately 20 caudal vertebrae and not less than 24 in the abdominal region. I agree that there are approximately 20 caudal vertebrae, but the abdominal region contains at least 35; the total number of vertebrae is between 55 and 65.

All centra are as deep as long, amphicoelous and pierced centrally by a large canal for the notochord. The centra are ornamented by a complex system of anastomosing ridges which impart a spongy appearance to some of the caudal centra.

The neural arches are autogenous throughout the abdominal region but are fused with the centra in the caudal region. Throughout most of the abdominal region epineurals are fused with the neural arches. In the posterior abdominal and caudal regions epineurals appear to be absent. At least the first 25 abdominal centra bear autogenous parapophyses, which are ovoid in shape. Behind this level, the parapophyses are fused with the centra and become longer, with a facet developed on the posterior face. The pleural ribs are narrow and slightly curved; they only partially encircle the abdominal cavity, as is usual in fishes with a rounded body. Ribs are absent from the first centrum.

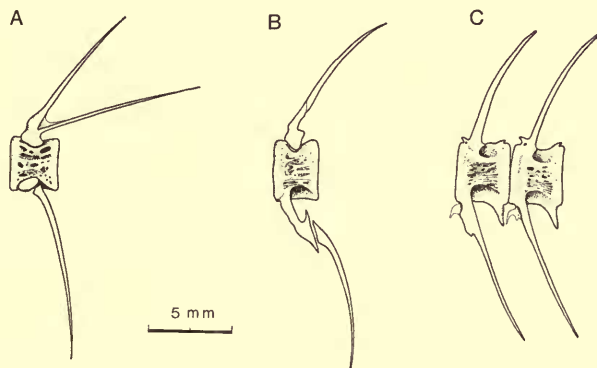


FIG. 22. *Rhacolepis buccalis* Agassiz. Vertebrae in left lateral view: A, from anterior abdominal region; B, from posterior abdominal region; C, from mid-caudal region.

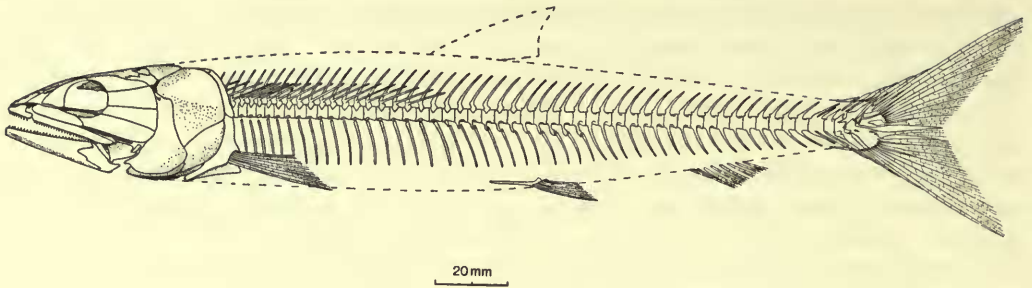


FIG. 23. *Rhacolepis buccalis* Agassiz. Entire fish, scales omitted.

The haemal arches are fused with the caudal centra. The neural and haemal arches of the caudal region bear anterior zygapophyses and there are also ventral posterior zygapophyses (Fig. 22C).

Dorsal and anal fins. The dorsal and anal fins are very poorly known. UA 12026 shows that the dorsal fin originates above the thirtieth vertebra which is probably located at the centre of the back (occiput-caudal peduncle). There are approximately 14 pterygiophores suggesting about 16 fin-rays. The first pterygiophore is distinctive in bearing a large membranous expansion. The base length of the dorsal fin is equal to the length of five and a half centra. The shape of the dorsal fin is unknown.

The anal fin is even more poorly known; it appears (UA 12027) to originate slightly nearer to the pelvics than the caudal peduncle. At least 7 fin-rays are present. Woodward (1887: 538) suggests there are about 10 anal fin-rays.

Caudal skeleton and fin. The caudal fin-rays are supported by structures associated with two ural and three preural centra (Fig. 24A). The parhypural bears a small hypurapophysis but is otherwise similar to that seen in *Notelops*. The lower hypurals are fused (or partially fused) to one another and to the rather small first ural centrum (Fig. 24, $U_1 + H_1 + H_2$). At least two upper hypurals can be identified (Fig. 24B, H_3, H_4) H_3 being somewhat expanded distally. There are two uroneurals (Fig. 24, Un_1, Un_2), the first of which is deeply forked proximally and partially overlies the first preural centrum. The first uroneural also bears a small anterior projection. There are neural arches associated with the first and second preural centra, each fused to the supporting centrum. Two epurals are present. In three of four specimens in which the vertebrae in the caudal peduncle region were observed, the third preural centrum was seen to be a compound element (Fig. 24A, Pu_{3+4}) bearing two neural and haemal spines. The significance of this is not clear but similar 'double vertebrae', immediately in front of the caudal peduncle, are frequently seen in cyprinid caudal skeletons.

There are 19 principal fin-rays, the innermost of each lobe with expanded bases. Preceding the uppermost principal ray there are five procurrent rays and a dorsal caudal scute. Preceding the lowermost principal ray there are four procurrent rays and a ventral caudal scute.

Squamation. Cycloid scales cover the body and the bases of the caudal, dorsal and anal fins. The scales are thin and ovoid, being deeper than long. The scales covering the anterior part of the trunk are noticeably larger than those posteriorly. The dorsal and ventral fields are marked by evenly spaced circuli. In the anterior field the circuli break up into ridges without any definable pattern. The posterior field is marked by many fine, radiating ridges. Bone-cell spaces are present in the anterior field. In many specimens the scales are partially abraded and the posterior

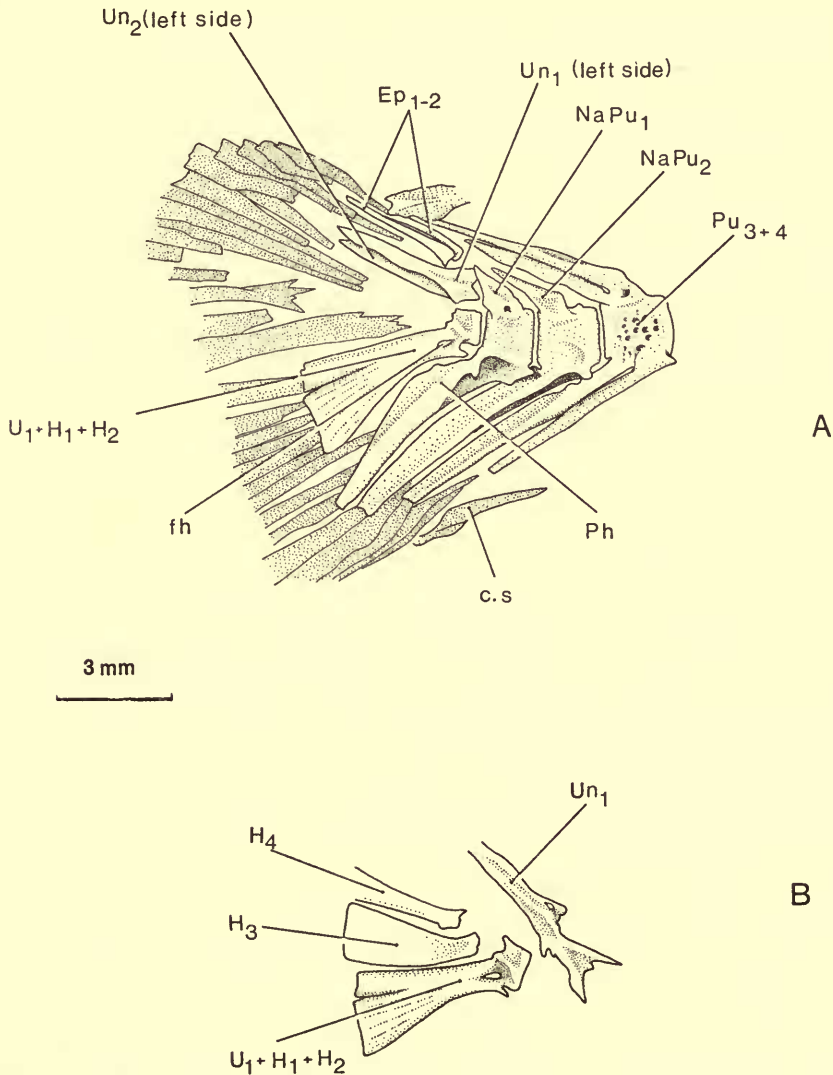


FIG. 24. *Rhacolepis buccalis* Agassiz. A: Caudal skeleton and fin in right lateral view. Camera lucida drawing of UA 12027. B: Uroneural and hypurals in right lateral view. Camera lucida drawing of UA 12026.

margins often have a crenulated appearance. Indeed, such a preservation led Agassiz (1844) to assign *Rhacolepis* (including *Notelops*) to his order Ctenoides.

A complete lateral line scale count could not be made but there are estimated to be about 90. The transverse count in front of the dorsal fin is about 10 above and about 11 below the lateral line row. The lateral line scales bear a tube, which is only seen in well-preserved specimens. A large, pointed pectoral axillary scale is present and above this, in the same transverse row, there is another large but less pointed scale.

Other species of Rhacolepis. Agassiz (1841 : 83) described *Rhacolepis latus* (generic name incorrectly spelled *Phacolepis*) from the same formation and locality as the type species. Woodward (1887 : 539 ; pl. 47, fig. 5) described this form more completely. The type specimen (BM(NH) P.1959) is distorted and there is some degree of post mortem anteroposterior compression, so that the true position of the fins is unknown. Jordan (1921 : 68) doubts the validity of this species. As can be seen from Woodward's figure the operculum is deep and shows a convex ventral margin, unlike *R. buccalis* but similar to *Brannerion vestitum*. The validity of this species must remain in doubt.

A third species, *Rhacolepis defiorei*, is described by d'Erasmus (1938), from the Santana Formation, Ceará, Brazil. I have not seen any of the material on which this species is based and do not therefore comment on its status. Santos & Valença (1968 : table 1) recognize all three species, *R. buccalis*, *R. latus* and *R. defiorei*.

Genus *PACHYRHIZODUS* Dixon 1850

1850 *Pachyrhizodus* Dixon : 374.

1872 *Thrissopater* Günther : 1.

DIAGNOSIS (emended). Pachyrhizodontid fishes in which the skull roof is marked with a frontal depression, dermethmoid broad, dilatator fossa with a roof posteriorly, pterotic not produced into a spine ; exoccipitals meeting above but not below foramen magnum, endochondral elements of the otic region of the braincase united by interdigitating sutures, no fenestra between autosphenotic and pterotic, foramen for the orbital artery and the posterior opening of the jugular canal close together on the lateral face of prootic and enclosed within a ' prootic cup ' ; anterior ceratohyal with or without fenestra ; posterior infraorbitals usually very broad, overlying preoperculum and often much of the operculum ; preoperculum expanded postero-ventrally and with tapered vertical limb, preopercular sensory canal profusely branched, operculum with oblique ventral margin, interoperculum longer than deep ; ventral postcleithrum expanded posteriorly, outer pectoral fin-ray large and closely articulated ; caudal fin-rays (where known) crossing hypurals at a steep angle.

TYPE SPECIES. *Pachyrhizodus basalis* Dixon.

REMARKS. The two genera *Thrissopater* Günther and *Pachyrhizodus* Dixon are generally recognized as being very similar. Woodward (1901) in diagnosing them implied that they may be distinguished by two features : *Thrissopater* shows a frontal depression which is absent in *Pachyrhizodus* ; *Pachyrhizodus* bears an inner

tooth on the premaxilla whereas there is no inner tooth in *Thrissopater*. Woodward (1908) later referred *Thrissopater magnus* Woodward to the genus *Pachyrhizodus* and stated that the latter genus does, in fact, exhibit a frontal depression. The only feature separating the two genera would seem to be the presence of an inner premaxillary tooth in *Pachyrhizodus*.

The presence or absence of an inner premaxillary tooth is very difficult to verify in the specimens referable to *Thrissopater salmoneus* Günther and *Thrissopater megalops* Woodward. Specimens of *T. salmoneus* are poorly preserved in Gault Clay and those that show the premaxilla are not preparable. One specimen, BM(NH) 47199, does show a large tooth close to the imperfectly preserved premaxilla. This tooth has much the same form as the inner premaxillary tooth of *Pachyrhizodus subulidens* (Owen). No specimen of *Thrissopater megalops*, except the holotype, shows a premaxilla and consequently it is difficult to check the condition here. In view of the fact that *Thrissopater* and *Pachyrhizodus* are similar in all other cranial characters and there is no clear-cut difference between them, I propose to include *Thrissopater* within the genus *Pachyrhizodus*.

The following description is based upon *Pachyrhizodus megalops* (Woodward). The choice of this species, as representative of the genus, was governed by the availability of a cranium that could be prepared in acid. In some respects this choice is unfortunate since *P. megalops* is known to differ from other species in the large orbit and the differentiation of the teeth along the length of the jaws. However, the braincase and other cranial features of *P. megalops* agree closely with those of other English species represented by cranial material, *P. magnus* and *P. subulidens*.

Pachyrhizodus megalops (Woodward)

(Figs. 25-31)

1901 *Thrissopater megalops* Woodward : 35 ; pl. 7, fig. 4.

1908 *Thrissopater megalops* Woodward : 136 ; pl. 28, fig. 5.

DIAGNOSIS (emended). Small species of *Pachyrhizodus* in which the width of the skull roof at the level of the autosphenotic is equal to its width at the occiput ; diameter of the orbit equal to approximately 55 per cent of neurocranial length ; posterior infraorbitals narrow, not covering preoperculum ; marginal teeth on premaxilla (c. 6 mm long) three times as long as those on the maxilla ; anterior teeth on dentary as large as the premaxillary teeth, but decreasing in length posteriorly ; teeth straight ; premaxilla with approximately 10 marginal teeth ; maxilla with approximately 35 teeth ; dentary without inflected ventral margin.

HOLOTYPE. BM(NH) 40826, incomplete head, Lower Chalk (Zone of *Holaster subglobosus* - Upper Cenomanian), Sussex, England.

MATERIAL. The holotype and BM(NH) 16328 (prepared in acid), GSM temporary number (TN) 5738. The last-mentioned specimen is the property of the Dorking Museum but is retained in the Institute of Geological Sciences (Geological Survey Museum), London.

FORMATION AND LOCALITY. Lower Chalk (Cenomanian), Sussex, England.

DESCRIPTION. *Braincase*. The skull roof is broad, the greatest width, at the level of the autosphenotic spines, equal to half the length of the braincase. The braincase is deep, the maximum depth occurring at the angle of the parasphenoid and being nearly equal to half the braincase length. It is not known if all species of *Pachyrhizodus* have a deep neurocranium. *Pachyrhizodus megalops* has a large orbit (diameter equal to half the braincase length) and perhaps this causes the neurocranium to be deep (Forey 1973b : 66). Other English species of *Pachyrhizodus* have relatively smaller orbits.

The skull roof is flat above the orbit, raised at the centre of ossification of each frontal and markedly convex in the otic region. Although the extreme tip of the snout is missing in all specimens, it appears to have been rather blunt.

The dermethmoid (Fig. 25, De) is broad and is marked by fine ridges. The margin of the dermethmoid is poorly known. In ventral view (Fig. 29) the dermethmoid is raised into anteromedially directed 'tubes', which make an impression on the dorsal surface anteriorly. There is no trace of an ethmoid commissure (cf. *Notelops*). The bone is very thin. In *P. megalops* there is no mesethmoid but in *P. subulidens* (Owen) the mesethmoid is a spongy ossification. The dermethmoid of the latter species is unknown.

The frontals form a very large proportion of the skull roof. They are medially united throughout their length by a suture which becomes sinuous in the epiphyseal region, as in *Rhacolepis*. At this level there is a shallow median depression and may also be a transverse ridge running between the centres of ossification of the frontals. In *P. salmoneus* (Günther) and *P. subulidens* this depression and the transverse ridges are particularly well developed. The depression is probably a growth phenomenon and of little taxonomic significance; it may also be seen in large specimens of *Chanos* (Ridewood 1905 : fig. 140A).

Each frontal (Fig. 25, Fr) is broad above the orbit but becomes narrower posteriorly. The lateral margin is excavated above the autosphenotic spine and there is no roof over the dilatator fossa, a situation comparable to that seen in *Rhacolepis*. The frontal is marked by ridges which radiate from the raised centre of ossification. The ridges running toward the anterolateral limit of the frontal are particularly well developed. The supraorbital sensory canal runs within the most pronounced of these ridges and opens on to the surface above the lateral ethmoid. A nasal could not be identified. Posteriorly, the supraorbital sensory canal has two branches: one runs laterally from the centre of ossification and opens to the surface above the autosphenotic spine; another runs back and opens immediately anterior to the frontal/parietal contact. It proved impossible to determine if there was a connection between the supraorbital and infraorbital canals. A few, small, medially directed branches occur in front of the centre of ossification of the frontal.

The parietal (Fig. 25, Pa) is small, considerably wider than long, and is separated from its partner by the supraoccipital (Figs 25, 27, Soc). The latter element is marked dorsally by radiating ridges. The supraoccipital crest is very small. The supratemporal sensory canal (Fig. 27, f.stt.com) ran transversely through the dorsal limit of the crest. Near the top of the crest there is a foramen (Fig. 27, f.p.f) on

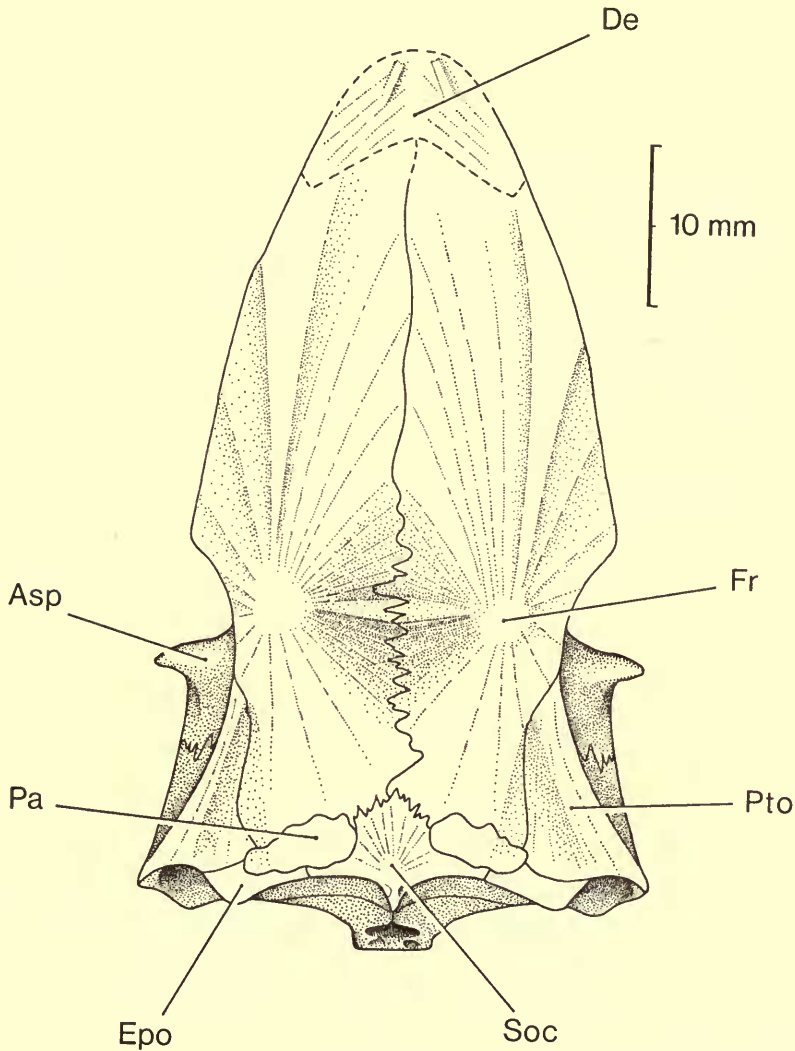


FIG. 25. *Pachyrhizodus megalops* (Woodward). Braincase in dorsal view. Based on BM(NH) P.16328.

either side of the midline, which leads from the posterior face of the braincase into the lumen of the post-temporal fossa. The function of this foramen is unknown; its small size would suggest that it is not involved with musculature. It is possible that a tendon or nerve may have passed through here. A foramen in a similar position has been observed by Dr C. Patterson (personal communication), piercing the supraoccipital of *Rhacolepis*. I have also seen a foramen in the same position on one side of the supraoccipital crest of one specimen of *Notelops* (UA 12021). Below the skull roof the supraoccipital is produced as two anterolaterally directed

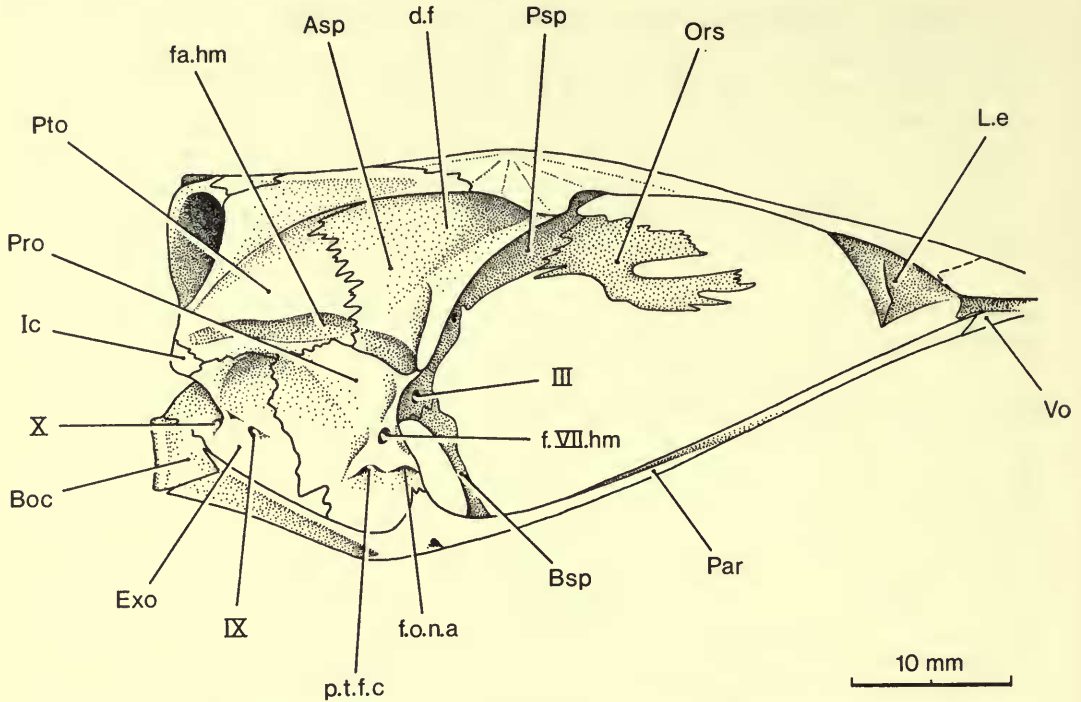


FIG. 26. *Pachyrhizodus megalops* (Woodward). Braincase in right lateral view. Based on BM(NH) P.16328.

wings. This results in a cup-shaped depression which is open anteriorly and covered by the frontals.

The epiotic (Figs 25, 27, Epo) is small and the epiotic process poorly developed. In the posterior view the epiotic may be seen to form the dorsomedial margin of the opening to the post-temporal fossa. This rim of the epiotic is thickened and suggests the usual course of the posterior semicircular canal through the epiotic.

The pterotic (Figs 25, 26, 27, Pto) forms the posterior half of the unroofed dilatator fossa and the greater proportion of the hyomandibular facet. The pterotic of *Pachyrhizodus megalops* is not produced as a posterior spine as it is in *Rhacolepis*. The dorsal surface of the pterotic bears a shallow groove, the inner areas of which continue on the frontal and parietal. A similar, but better-developed, groove is seen on the pterotic of *Esocelops cavifrons* Woodward. It is possible that a thin sliver of epaxial musculature lay in this groove. In posterior view the pterotic may be seen to form the lateral wall of the post-temporal fossa.

The intercalar (Figs 26, 27, Ic) is large and caps the junction between the epiotic, pterotic and exoccipital. Most of the intercalar is found on the posterior face of the neurocranium, where it forms part of the floor and the ventromedial margin of the opening to the post-temporal fossa. A prootic-intercalar bridge is absent.

The autosphenotic (Figs 25, 26, 28, 29, Asp) is large and bears a prominent autosphenotic spine, the true extent of which may only be seen in lateral view. The

autosphenotic forms much of the dilatator fossa, which is large in this species. The anterior third of the hyomandibular facet is formed by the autosphenotic. A foramen for the otic branch of the facial (Fig. 28, f.VII.ot) pierces the orbital face of the autosphenotic. The zigzag suture pattern between the autosphenotic and pterotic (Fig. 28) is more like that in *Rhacolepis* than *Notelops*. The inner surface of the autosphenotic forms the anterior wall of the post-temporal fossa.

The exoccipital (Figs 26, 29, Exo) meets its antimere above, but not below, the foramen magnum. The foramina for the vagus and glossopharyngeal nerves lay close together, as in *Rhacolepis*. The anterodorsal region of the lateral face of the exoccipital is concave, and with an adjacent concavity in the prootic forms a shallow depression in the position of a subtemporal fossa. The size of this depression does not merit the term 'fossa'. The basioccipital (Figs 26, 27, 29, Boc) is similar to that element in *Rhacolepis*. It is relatively small, and bears paired dorsal depressions suggesting that a neural arch articulated with the basioccipital. The basioccipital forms part of the foramen magnum.

The prootic (Figs 26, 28, 29, Pro) also bears certain resemblances to the prootic of *Rhacolepis*, in that the foramen for the trigeminal (Fig. 28, V) is separate from the anterior opening of the jugular canal (Fig. 28, a.t.f.c). The foramen for the oculomotor (Fig. 28, III) is situated medial to the trigeminal foramen (a slight difference from the condition in *Rhacolepis*, p. 150) and a separate foramen for the profundus

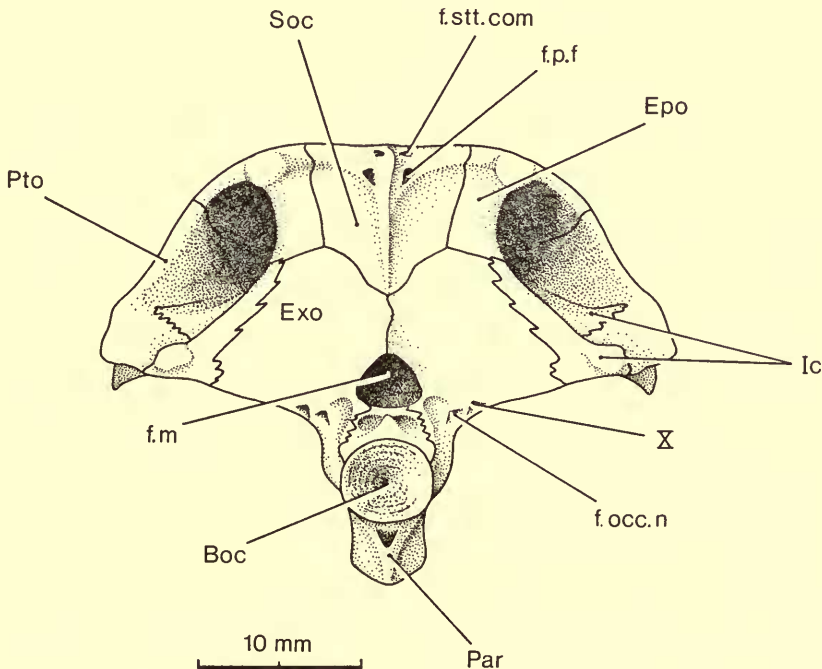


FIG. 27. *Pachyrhizodus megalops* (Woodward). Braincase in posterior view. Based on BM(NH) P.16328.

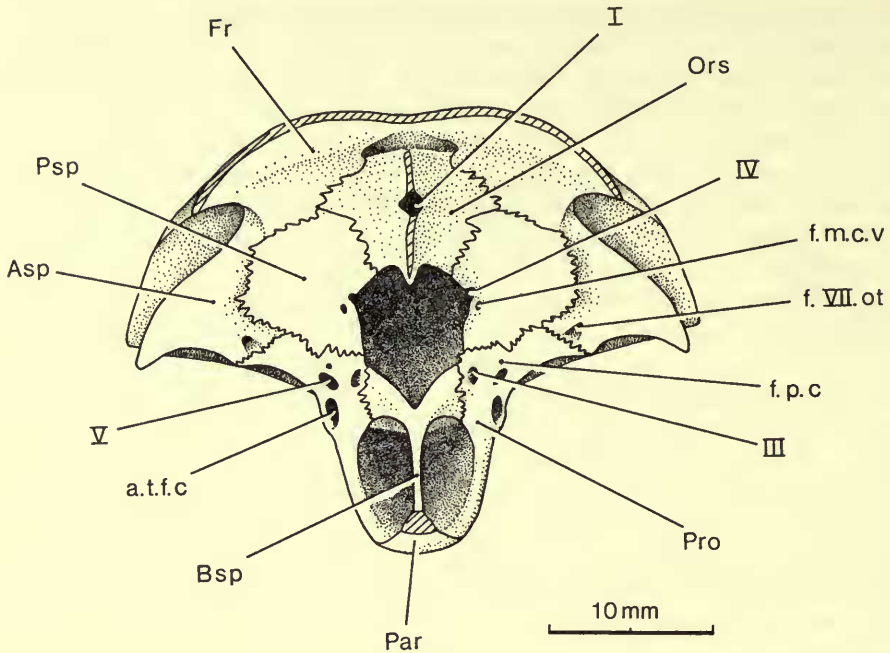


FIG. 28. *Pachyrhizodus megalops* (Woodward). Postorbital parts of the braincase in anterior view. Based on BM(NH) P.16328.

ciliaris (Fig. 28, f.p.c) is located above the trigeminal foramen. The lateral face of the prootic is different from that of *Rhacolepis* and *Notelops*. The foramen for the hyomandibular branch of the facial (Fig. 26, f.VII.hm) is situated in the lateral wall of the jugular canal. From the point of exit the hyomandibular branch ran dorsally in a deep groove on the prootic before turning posteriorly and laterally to pierce the medial face of the hyomandibular. The posterior opening of the jugular canal (Figs 26, 29, p.t.f.c) and the foramen for the orbital artery (Figs 26, 29, f.o.n.a) are very close together. Both of these ventral openings are embraced by a ridge of bone resulting in a cup-shaped structure, here termed the prootic cup. In *Rhacolepis* there is a ridge of bone connecting the widely separated openings of the jugular canal and the arterial foramen. In comparison with *Rhacolepis* the opening of the jugular canal in *P. megalops* has 'moved' anteroventrally and the connecting ridge has become shorter. In ventral view (Fig. 29) a small foramen may be seen opening into the anterior end of the prootic cup. This foramen leads into a short canal which joins with the canal for the orbital artery. It is possible that this small foramen was occupied by a posterior palatine branch of the facial. A prootic cup can be identified in *P. magnus* and is probably a generic character. The suture lines between the prootic and the adjacent exoccipital, autosphenotic, parasphenoid and basisphenoid are zigzag in shape.

The pterosphenoid (Figs 26, 28, 29, Psp) lies dorsal to the anterior (orbital) face of the prootic. The inner margin of the pterosphenoid forms part of the wall of

the optic foramen. The inner margin is excavated for the passage of the trochlear (as in *Rhacolepis*) and there is a small foramen for the middle cerebral vein. The sutures between the pterosphenoïd and neighbouring bones are of a complex zigzag form. The suture between the pterosphenoïd and autosphenotic is rather unusual, the surface of the pterosphenoïd being raised with respect to the autosphenotic.

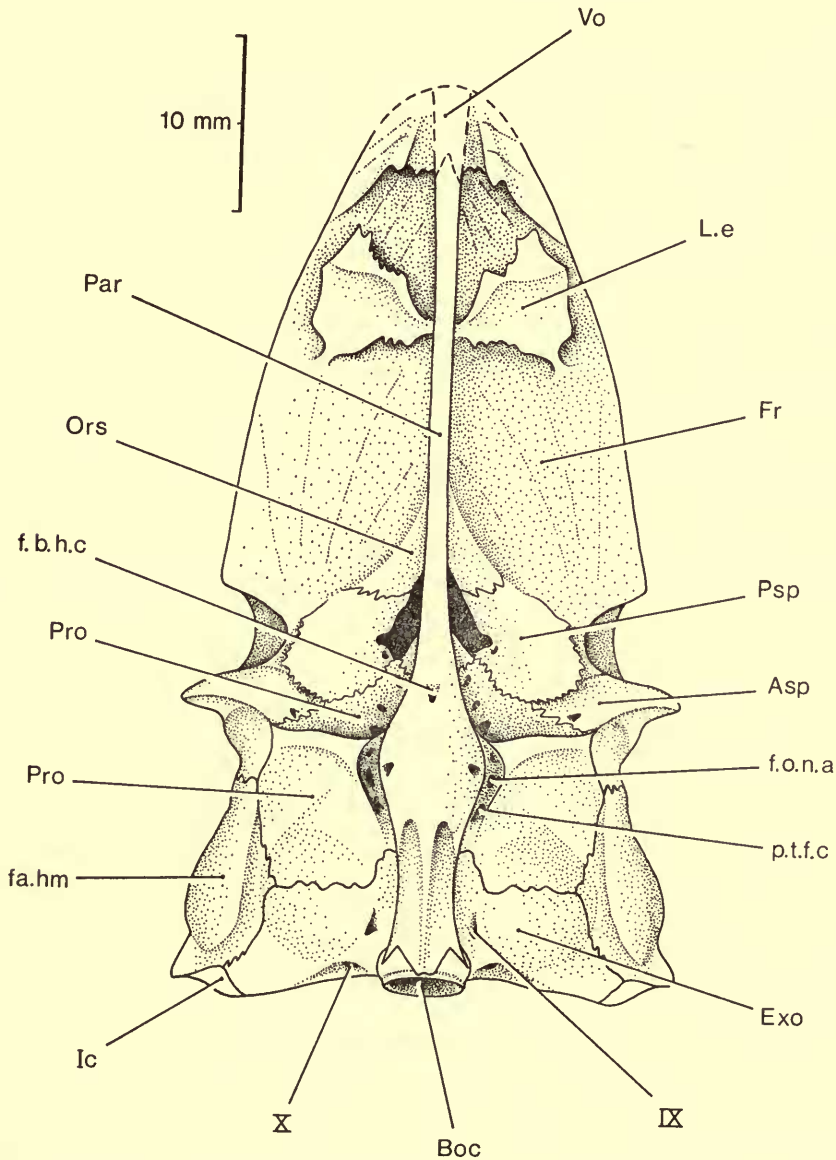


FIG. 29. *Pachyrhizodus megalops* (Woodward). Braincase in ventral view. Based on BM(NH) P.16328.

This results in a groove which follows this suture and marks the path of the superficial ophthalmic branches of the trigeminal and facial.

The orbitosphenoid (Figs 26, 28, 29, Ors) forms the dorsal margin of the optic foramen and meets ventral flanges of the frontals dorsally and the pterosphenoids laterally. The olfactory tracts passed out through a deep excavation in the orbitosphenoid. The basisphenoid (Figs 26, 28, Bsp) forms the ventral margin of the optic foramen and is produced ventrally as a slender pedicel to contact the parasphenoid.

The parasphenoid (Figs 26, 27, 28, 29, Par) is long and angled beneath the prootic cup. Beneath the orbit the parasphenoid is narrow. The ascending wings are poorly developed. Posteriorly the parasphenoid becomes deeper and is marked by a groove on either side. There is a small posterior opening to the myodome, which lies between the parasphenoid and the basioccipital. This may be seen in Fig. 27. At the level of the ascending wing there is a foramen for the internal carotid artery and beneath the basisphenoid insertion there is a median foramen for the buccohypophyseal canal (Fig. 29, f.b.h.c). In all, the parasphenoid of *P. megalops* is very similar to that of *Rhacolepis*. The vomer (Figs 26, 29, Vo) is small but the precise limits of this element are unknown. The lateral ethmoid (Figs 26, 29, L.e) is represented by perichondral bone. Dorsally the lateral ethmoid contacts the frontals by a very narrow pedicel. Ventrally the lateral ethmoid expands in both transverse and parasagittal planes. No foramen in the transverse wall could be seen; the olfactory tract and nasal artery presumably passed through cartilage medial to the lateral ethmoid.

Dermal upper jaw. The upper jaw is long and reaches back to a level beneath the posterior limit of the orbit. The jaw is formed by the premaxilla, maxilla and

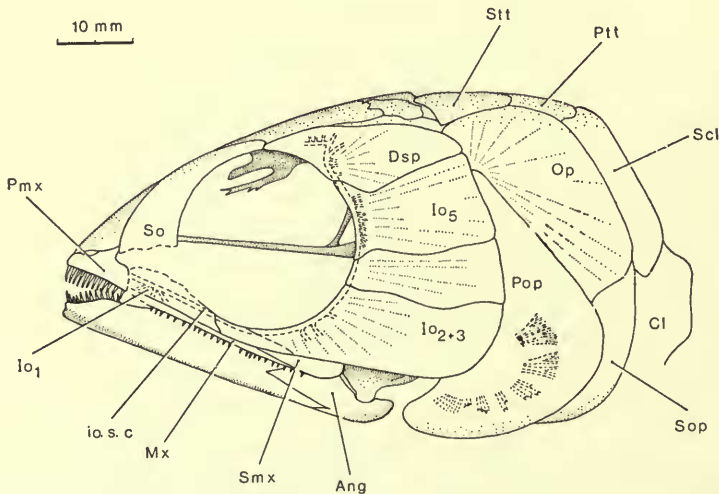


FIG. 30. *Pachyrhizodus megalops* (Woodward). Restoration of cranium in left lateral view.

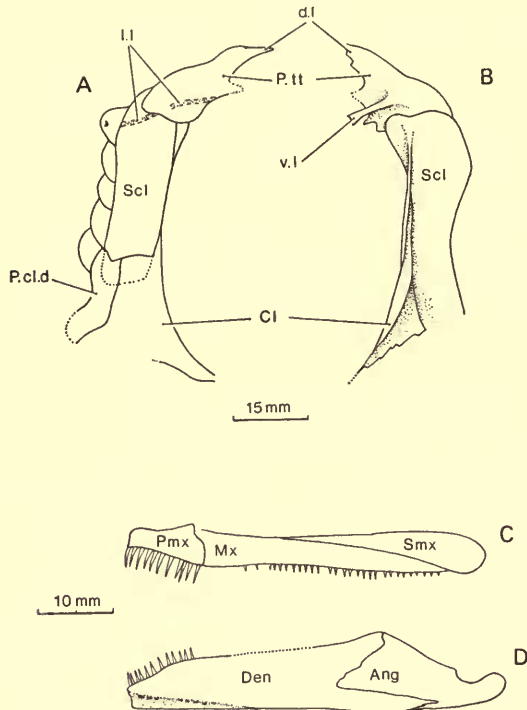


FIG. 31. *Pachyrhizodus megalops* (Woodward). A, B: Restoration of upper part of right pectoral girdle in lateral and medial views. C: Restoration of left upper jaw in lateral view. D: Restoration of left lower jaw in lateral view.

a single supramaxilla. The premaxilla (Fig. 30, Pmx) is small, equivalent in length to one-fifth of the total length of the upper jaw. The premaxilla is narrow anteriorly where it contacts its partner in the midline but becomes deeper posteriorly where it overlaps the head of the maxilla. A dorsal process on the premaxilla fits tightly against the dermethmoid. There are 9-11 long, needle-like premaxillary teeth.

The maxilla (Fig. 30, Mx) is long and shallow and fits tightly against the premaxilla anteriorly. Although the morphology of the premaxillary/maxillary overlap is not known in *P. megalops* I suspect it is similar to that seen in *P. subulidens* which is described below (p. 173). There are approximately 35 maxillary teeth set in a single row. Each maxillary tooth is less than half the length of a premaxillary tooth and is slightly stouter. As in *Notelops* and *Rhacolepis* there is a narrow ledge of bone lateral to the bases of the maxillary teeth.

Lower jaw. This is poorly known; it is only partly seen in lateral view in the specimens examined. The dentary (Fig. 31, Den) occupies nearly two-thirds of the lower jaw length. The anterior end of the dentary is truncated at the symphysis, from which the oral margin curves upwards for a distance before levelling off and passing backwards to the weakly-defined coronoid process. In the holotype there

are 12 needle-like teeth in the anterior third of the oral margin of the dentary. An entire oral margin was not seen in any dentary so it is not known whether the tooth row extended back to the coronoid process. However, there are a few small teeth immediately anterior to the coronoid process in GSM (TN) 5738. The ventrolateral margin of the dentary is grooved. Within this groove, at the anterior end of the dentary, there are seven pores marking the path of the mandibular sensory canal.

The lateral face of the posterior third of the lower jaw is formed by the angular (Fig. 31, Ang). However, the medial aspect of the jaw is not known and therefore it is possible this bone should be termed an angulo-articular. The angular forms the lateral part of the articulating cup and is produced posteriorly as a retroarticular process.

Circumorbital series. This is composed of six (possibly seven) bones and completely surrounds the orbit. The supraorbital (Fig. 30, So) is very large, contacting the dermosphenotic posteriorly and curving anteroventrally to the tip of the premaxilla. The supraorbital lies tightly against the underlying lateral ethmoid.

The first infraorbital (Fig. 30, Io₁) is imperfectly displayed in GSM (TN) 5738. It is slightly expanded anteriorly and meets the infraorbital behind in an oblique suture. The presence of a second infraorbital cannot be demonstrated with confidence; it could well be fused with the third infraorbital, as it appears to be in *Notelops* and *Rhacolepis*. The third infraorbital (Fig. 30, Io₂₊₃) is, as usual in many lower teleosts, a large element forming the posteroventral margin of the orbit. The fourth and fifth (Fig. 30, Io₄) are rectangular, being broader than deep. The dermosphenotic (Fig. 30, Dsp) is large and triangular and completely covers the dilatator fossa, as in *Rhacolepis*.

The infraorbital sensory canal runs at the orbital margin for much of its length. Anteriorly the sensory canal runs through the centre of the first infraorbital and gives off four ventral branches. Within the third infraorbital there are three branches, while in the fifth infraorbital there are many branches but not all of these open to the surface. Within the dermosphenotic the main sensory canal runs dorsally and gives off a blindly-ending anterior branch and a posterior branch which opens to the surface. There are also several smaller branches which may be seen in Fig. 30. The infraorbital sensory canal of *P. megalops* is remarkable for the prolific branching in the dermosphenotic and the fifth infraorbital.

Opercular series. Compared to *Rhacolepis*, the operculum (Fig. 30, Op) of *P. megalops* is narrow and the preoperculum (Fig. 30, Pop) overlaps much of the operculum and suboperculum. The preopercular sensory canal is (like the infraorbital canal) profusely branched. These branches are arranged in six groups (Fig. 30) in BM(NH) P.10219; they are more evenly arranged in GSM (TN) 5738. An interoperculum was not seen in *P. megalops*.

Postcranial skeleton. Little is known of the postcranial skeleton. One specimen, GSM (TN) 5738, shows a few vertebrae. The ornamentation of the centra is confined to a few longitudinal grooves. In this *P. megalops* is similar to other smaller species such as *P. salmoneus* (Günther) and *P. subulidens* (Owen) but different from larger species such as *P. dibleyi* Woodward and *P. basalis* Dixon in which the surface of the vertebrae is smooth.

Of the shoulder girdle, the post-temporal, supracleithrum and part of the cleithrum are known in *P. megalops*. Significant points are the broad post-temporal and the spine-like tip of the cleithrum which reaches well up the medial surface of the supracleithrum (Fig. 31B). Neither of these features is seen in *Notelops* nor *Rhacolepis*. The only part of the pectoral fin known is the outer ray. It is stout and closely articulated. The holotype of *P. salmonesus* shows a similar stout outer pectoral fin-ray.

Squamation. The scales of *P. megalops* are cycloid, almost circular and 5–6 mm in diameter. The anterior and lateral fields are marked by fine, evenly-spaced circuli. The posterior field is marked by small tuberculations which are arranged to give the appearance of fine, longitudinal ridges.

Other English species of *Pachyrhizodus*

Woodward (1907, 1908) describes material of *Pachyrhizodus* (and *Thrissopater*) from the English Chalk. The following notes supplement that work.

In addition to *P. megalops* two further species of the genus are reasonably well known from cranial remains, *P. subulidens* (Owen) and *P. magnus* (Woodward). Both exhibit a skull roof that is similar to that of *P. megalops*. In *P. subulidens* (Woodward 1908 : fig. 39 ; pl. 27, fig. 1a) the frontals above the orbit and the dermethmoid are particularly broad and the depressions on the skull roof are large. In both species the dilatator fossa is more extensively roofed than in *P. megalops* and the parietals are relatively smaller. The circumorbital series is similar to that of *P. megalops* in being composed of a large supraorbital (antorbital of Woodward 1908) followed by five infraorbitals. However, the orbit is smaller and the posterior infraorbitals are very broad and become very thin at their posterior margins. In *P. subulidens* the preoperculum is expanded posteroventrally and, with the large posterior infraorbitals, virtually covers the operculum and suboperculum.

The premaxilla of *P. magnus* (Woodward 1908 ; pl. 28, fig. 1) is deeper than in *P. megalops* and the dorsal process is better developed. The premaxillae of the larger species (*P. basalis* Dixon and *P. dibleyi* Woodward) are not found associated, but the angle of tooth implantation shows that the outer surface of the premaxilla must have been held almost horizontally. The premaxilla/maxilla overlap is known in *P. subulidens* (Fig. 32). The premaxilla fits into a shallow notch in the lateral face of the maxilla. The medial surface of the premaxilla has a well-developed ridge fitting into this notch. This premaxilla/maxilla overlap must limit independent movement between these bones. Anteriorly, there is a small facet (Fig. 32, fa.eth) for articulation with the ethmoid ; in this species there is a small mesethmoid.

The morphology of the mandibular ramus varies between the different species, the chief variation being in the dentition (see diagnoses). It is of interest to note that in *P. subulidens* and *P. magnus*, in which complete rami are known, the lateral expression of the angular (? angulo-articular) is very small compared to that of the dentary. This is also observed in *Notelops* and *Rhacolepis*. The dentary of the larger species (*P. basalis* and *P. subulidens*) shows a strongly inflected ventral margin, not seen in *P. megalops*.

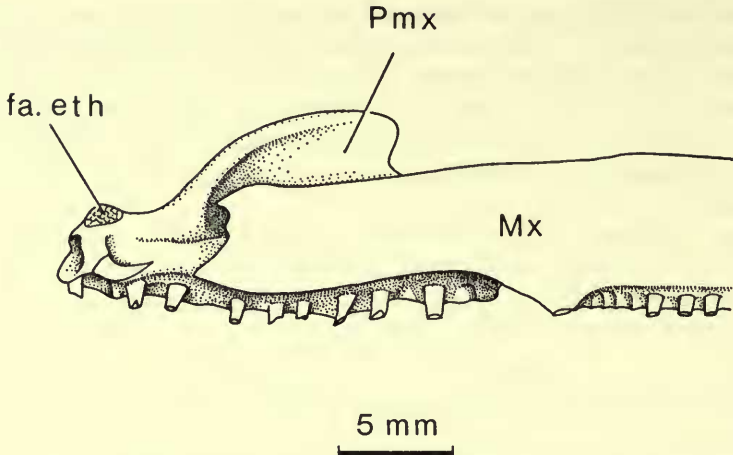


FIG. 32. *Pachyrhizodus subulidens* (Owen). Freehand sketch of right premaxilla and head of maxilla in medial view. Based on BM(NH) P.4298.

The caudal skeleton and fin of the English species of *Pachyrhizodus* are very poorly known. Woodward (1907: 124; pl. 26, fig. 6) suggested that BM(NH) P.5659, a specimen showing a posterior caudal region and caudal fin, is referable to *Pachyrhizodus*. The identity of this specimen is still in doubt and unfortunately the details of the endoskeleton are too poor to allow a critical assessment. However, the caudal fin-rays are closely segmented nearly to their bases. This feature is noted in *P. caninus* (Hay 1903: pl. 3). The holotype of *P. salmoneus* and an unregistered specimen of *P. subulidens* in the Sedgwick Museum, Cambridge, each show a small part of the caudal skeleton. In both the base of the first uroneural is much expanded and covers much of the first and second preural centra. These specimens also show that the upper principal fin-rays cross the fused upper hypurals at a steep angle.

There are many specimens (mostly jaw fragments) from the English Chalk which can be referred to the genus *Pachyrhizodus* and it seems worth while to attempt rediagnoses of the species. Details of jaw features are emphasized in so doing.

Pachyrhizodus salmoneus (Günther)

1872 *Thrissopater salmoneus* Günther: pl. 1.

1901 *Thrissopater salmoneus* Günther; Woodward: 33.

DIAGNOSIS (emended). Small species of *Pachyrhizodus* in which the width of the skull roof at the level of the autosphenotic is considerably less than the width of the skull roof at the occiput; diameter of the orbit equal to approximately 25 per cent of neurocranial length; posterior infraorbitals broad, covering much of the preoperculum; marginal teeth on premaxilla, teeth on maxilla and dentary of equal size (1-1.5 mm long) and slightly curved, premaxilla with approximately 10 marginal teeth and a single, large, straight inner tooth, maxilla with approximately 40 teeth;

dentary without strongly inflected ventral margin; approximately 50 vertebrae, marked by numerous fine ridges; scales small (c. 5 mm deep), not less than 35 in a transverse series anterior to the dorsal fin.

HOLOTYPE. SMB 42459, incomplete fish, Gault Clay (Albian) of Folkestone, Kent, England.

MATERIAL. The holotype and BM(NH) 47194, 47197, 47198, 47199, 47202, P.16, P.41, P.999 (2 specimens).

FORMATION AND LOCALITY. Gault Clay (Albian), Kent, England.

Pachyrhizodus magnus (Woodward)

1837 *Hypsodon lewesiensis* Agassiz : pl. 25a, fig. 1; pl. 25b, figs 4, 5 (errore).

1844 *Hypsodon lewesiensis* Agassiz 5 (1) : 100.

1901 *Thrissopater magnus* Woodward : 33; pl. 5, figs 1, 2.

1908 *Pachyrhizodus(?) magnus* (Woodward); Woodward : 131; pl. 28, fig. 1.

DIAGNOSIS (emended). Small species of *Pachyrhizodus* in which the width of the skull roof at the autosphenotics is nearly equal to its width at the occiput; diameter of the orbit equal to approximately 30 per cent of neurocranial length; posterior infraorbitals broad, covering much of preoperculum; marginal teeth on premaxilla and teeth on maxilla and dentary of equal or nearly equal size (1.5–2 mm long), teeth straight, premaxilla with approximately 14 marginal teeth and a single inner tooth which is only slightly larger than the marginal teeth, maxilla with approximately 40 teeth, dentary without strongly inflected ventral margin; vertebrae marked by a few small pits.

HOLOTYPE. BM(NH) 37981, incomplete head from Lower Chalk (probably Zone of *Holaster subglobosus* – Upper Cenomanian) of Kent, England.

MATERIAL. Only the holotype is known.

Pachyrhizodus subulidens (Owen)

(Fig. 32)

1840 *Raphiosaurus subulidens* Owen : 190.

1850 *Raphiosaurus lucius* Owen; Dixon : 385; pl. 39, figs 1–3.

1851 *Raphiosaurus subulidens* Owen : 19; pl. 10, figs 5, 6.

1889 *Pachyrhizodus subulidens* (Owen); Woodward : 351.

1901 *Pachyrhizodus subulidens* (Owen); Woodward : 43; pl. 7, figs 1, 2; pl. 5, fig. 2.

1908 *Pachyrhizodus subulidens* (Owen); Woodward : 129, fig. 39; pl. 27, figs 1–4.

? 1911 *Pachyrhizodus* sp. Woodward : 249; pl. 54, figs 2.

DIAGNOSIS (emended). Small species of *Pachyrhizodus* in which the width of the skull roof at the autosphenotic is nearly equal to its width at the occiput; diameter of the orbit equal to approximately 30 per cent of neurocranial length; posterior infraorbitals broad, covering much of the preoperculum; marginal teeth on premaxilla and teeth on maxilla of equal size (3–4 mm long), teeth on dentary much larger (6–7 mm long), all teeth on dermal jaw bones recurved, premaxilla with

approximately 10 marginal teeth and a single inner tooth which is only slightly larger than the marginal teeth, maxilla with 30-40 sockets, dentary with not less than 30 sockets; dentary with inflected ventral margin, the width of which does not exceed the depth of the dentary.

HOLOTYPE. SM B.9097, portion of maxilla from Lower Chalk (Zone of *Holaster subglobosus* - Upper Cenomanian), Cambridgeshire, England.

MATERIAL. The holotype, also SM B.94762a-c, B.94762d-j, B.94557, and BM(NH) 36635, 38566, 39079, 49078, P.1808, P.4298, P.6527, P.10812, P.11802, P.12896. The following are probably specimens of this species: BM(NH) 36138, 39087, P.4299.

FORMATION AND LOCALITY. Lower Chalk (Cenomanian), Cambridgeshire, Sussex and Kent, England.

Pachyrhizodus basalis Dixon

1837 *Hypsodon lewesiensis* Agassiz: pl. 25a, figs 2, 4; pl. 25b, figs 4-7.

1844 *Hypsodon lewesiensis* Agassiz 5 (1): 99.

1850 *Pachyrhizodus basalis* Dixon: 374; pl. 34, figs 9, 10.

1869 *Acrodonosaurus gardneri* Mason: 444; pl. 19.

1877 *Hypsodon lewesiensis* Agassiz; Newton: 508.

1888 *Pachyrhizodus gardneri* (Mason); Woodward: 314.

1901 *Pachyrhizodus basalis* Dixon; Woodward: 37.

1901 *Pachyrhizodus gardneri* (Mason); Woodward: 40.

1907 *Pachyrhizodus basalis* Dixon; Woodward: 125; pl. 25, figs 1, 2.

1907 *Pachyrhizodus gardneri* (Mason); Woodward: 125; pl. 25, figs 3-8; pl. 26, fig. 5.

DIAGNOSIS (emended). Large species of *Pachyrhizodus* in which the marginal teeth on the premaxilla are slightly larger than those on the maxilla, teeth on dentary larger than those on the upper jaw, marginal teeth on premaxilla and teeth on maxilla and dentary recurved, premaxilla with approximately 9 marginal teeth and one or two large inner teeth that may be slightly recurved or straight, dentary with 25-30 tooth sockets; dentary with strongly inflected ventral margin, the width of which exceeds the depth of the dentary.

HOLOTYPE. BM(NH) 49014, right maxilla, Lower Chalk (probably Zone of *Holaster subglobosus* - Upper Cenomanian) of Kent, England.

MATERIAL. The holotype, also SM B.94556 and BM(NH) 4105, 25791, 25792, 33256, 33257, 41671, 41674, 47236, 49757, 49905, P.5655, P.5656, P.9016, P.9697, P.10031, P.10044, P.11009, P.11908, P.12353, P.12892. The following are probably specimens of this species: SM B.40859, B.40860, B.40861, B.94555 and BM(NH) 4068, P.1808a, P.4506, P.5652, P.5653, P.5658.

FORMATIONS AND LOCALITIES. The majority of specimens are from the Lower Chalk (Cenomanian) of Surrey, Kent and Sussex, England. BM(NH) 4068 and 4105 are from the Middle Chalk (Zone of *Terebratulina lata* - Turonian) of Sussex, England. Woodward (1907: 128) notes that specimens are recorded from Upper Chalk (Zone of *Micraster coranguinum* - Santonian) of Surrey, England, but this could not be verified.

REMARKS. Woodward (1901, 1907) recognized two species, *P. basalis* Dixon and *P. gardneri* (Mason), which are here placed in synonymy under the prior name *P. basalis*. Woodward maintained that in *P. gardneri* the base of the inner premaxillary tooth reaches to the inner margin of the premaxilla and the tooth shows a slight inward curvature, while in *P. basalis* the inner premaxillary teeth are straight and the teeth bases stand away from the inner margin of the premaxilla. An examination of specimens referred to the two species shows that these features are within the limits of individual variation. In the absence of more complete material these species should therefore be considered synonymous.

Pachyrhizodus dibleyi Woodward

1901 *Pachyrhizodus dibleyi* Woodward : 38 ; fig. 3.

1907 *Pachyrhizodus dibleyi* Woodward : 128 ; pl. 26, figs 1-4.

DIAGNOSIS (emended). Large species of *Pachyrhizodus* known only by fragments of upper jaw, dentary and endopterygoid ; teeth of upper jaw large, conical, not recurved, posterior teeth in maxilla showing marked anteroposterior compression, teeth irregularly spaced ; teeth in lower jaw conical.

HOLOTYPE. BM(NH) P.9115, imperfect premaxilla and maxilla, Lower Chalk (Zone of *Holaster subglobosus* – Upper Cenomanian, Kent, England).

MATERIAL. The holotype, also BM(NH) 49093, P.4806, P.10042, and SM B.94564-5.

FORMATION AND LOCALITIES. Lower Chalk (Cenomanian), Kent, Surrey, and Sussex, England.

Other Species of *Pachyrhizodus*

Other species of *Pachyrhizodus* are known from North America and Australia. From North America, eight species of the genus have been described in works by Cope (1872, 1874, 1875), Loomis (1900) and Stewart (1898, 1899). Most of these species are based on isolated jaw fragments and it has become clear that there are, at most, two or three species involved. Applegate (1970) recognized three species, *Pachyrhizodus caninus* Cope, *P. kingi* Cope and *P. minimus* Stewart. Applegate (1970 : 411) noted that *P. kingi* may represent the juvenile form of *P. caninus*, but further remarked that the discontinuous size distribution and differences in the appearance of vertebral cross-sections may not support such a view. Dr David Bardack (personal communication) is also of the opinion that the American forms may be referred to two or, at most, three species.

The American species come from the Eagle Ford Shale, the Niobrara Chalk, the Austin Chalk, the Selma Chalk and the Mooreville Chalk. Together, these deposits range in age from Turonian to Campanian (Cobban & Reeside 1962, Stephenson *et al.* 1942). The American species are generally larger than most of the English species. The smallest, *P. minimus*, is approximately 900 mm long and is comparable to the estimated length of *P. subulidens*. The largest American species, *P. caninus*, is

over 1800 mm long and is probably about the same size as *P. basalis*. Both these American species are very similar to the larger English species. In both, the skull roof is broad throughout particularly above the orbit, the roof is formed of thick bone and the depression in the frontals (interfrontal fossa of Applegate 1970) is well developed, the preoperculum is expanded posteroventrally and is broadly rounded, and the posterior infraorbitals are very wide and cover much of the operculum and suboperculum. The jaws are also very similar in the English and American species. The premaxillae of the American species are held horizontally (or nearly so) and this resembles the presumed condition in *P. basalis* and *P. dibleyi*. The ventral margin of the dentary in the American species is strongly inflected as in some English species.

At present, comparisons between English and American species can only be made at a superficial level, but I know of no facts that would refute considering these species as being congeneric. A particularly strong similarity in skull proportions and jaw morphology exists between the English *P. subulidens* and the American *P. minimus*. A detailed study of the latter may well reveal it to be conspecific with *P. subulidens*.

There are two points of difference between the English and American species that have yet to be explained. The large 'scale-bone' which is reputed (Applegate 1970) to cover much of the operculum in the American species is not seen in the English species. This 'scale-bone' could, of course, be an enlarged supratemporal or possibly the large dermosphenotic. Secondly, the English species do not show the paired rounded tooth-plates (Applegate 1970: fig. 193c) that are either palatal or vomerine in origin. The vomer of the English species is relatively small and is certainly not a double structure while a tooth-bearing palatine has not yet been identified.

One species of *Pachyrhizodus* is known from Australia. *Pachyrhizodus marathonsensis* (Etheridge) from marine deposits of the Albian of Queensland has been described by Bardack (1962) and Bartholomai (1969). BM(NH) P.55858 is a specimen of *P. marathonsensis*. From the sketch (Fig. 33) of this specimen the typical *Pachyrhizodus* features may be seen: the frontal depression, large supraorbital, broad posterior infraorbitals, premaxilla with a broad dorsal process, small lateral expression of the angular, large preoperculum and the large outermost pectoral fin-ray. This specimen also shows a large basibranchial tooth plate and a spine-like anterior tip of the preoperculum, as in *Rhacolepis*. *Pachyrhizodus marathonsensis* is the only species in which a fenestrated anterior ceratohyal is recorded. Bartholomai (1969) suggests that *P. marathonsensis* is similar to *P. subulidens*, differing only in the narrower cranial roof and greater dorsal expression of the supraoccipital. Bartholomai (1969: 255) mentions that the nasals of *P. marathonsensis* are not preserved. In fact, nasals have not been described for any species of *Pachyrhizodus* and it is possible that nasals are absent from all species.

Mention must be made of *Thrissopater daguini* described by Arambourg (1954) from the Cenomanian of Jebel Tselfat, Morocco, although I have not seen either of the two specimens (Arambourg 1954: 70) of *T. daguini* and can add nothing to his description. Arambourg referred this form to *Thrissopater* because of certain

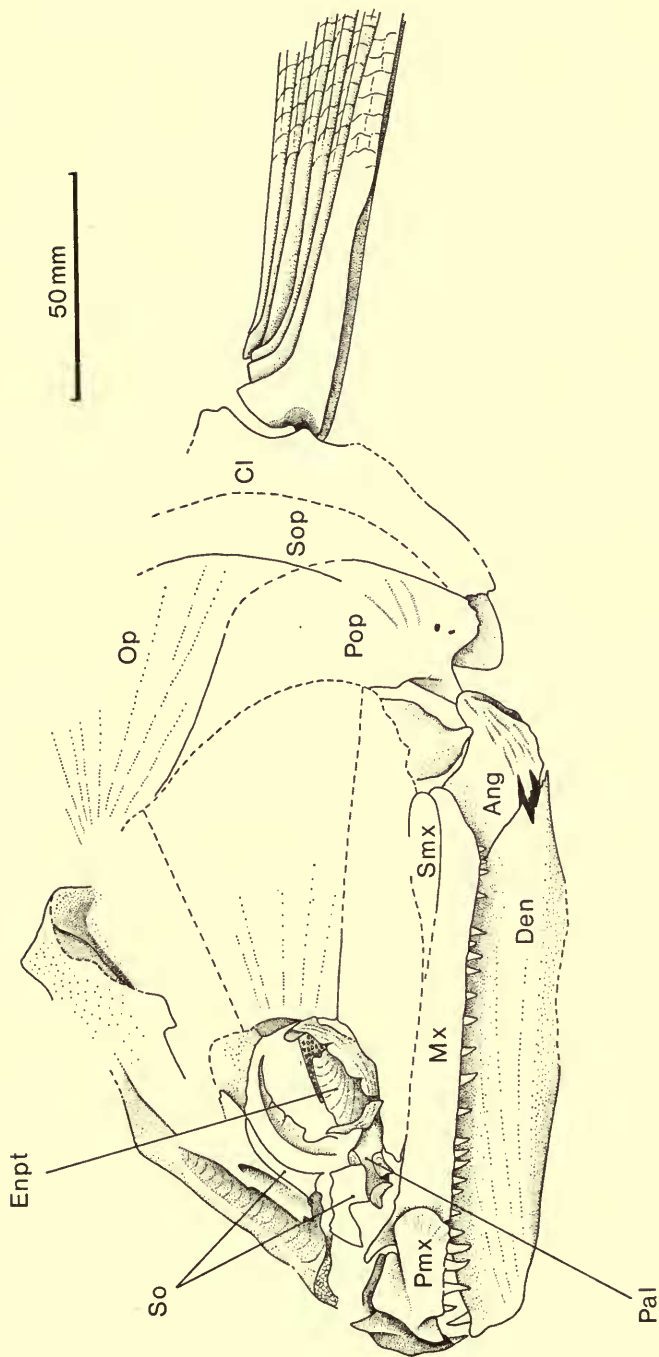


FIG. 33. *Pachyrrhizodus marathoniensis* (Etheridge). Freehand sketch of left lateral view of BM(NH) P.55858.

similarities in the skull roof, particularly the small separated parietals and the depression in the frontals immediately anterior to the supraoccipital. He went on to compare the skull roof with certain stomiatooids using similar characteristics.

Similarities in the small, separated parietals and the presence of a frontal depression do not constitute strong evidence of relationship. There are several marked differences between other species of *Thrissopater* (= *Pachyrhizodus*) and *T. daguini*. The skull roof of the latter shows that the frontals are narrow above the orbit, the pterotic is very small and the main supraorbital sensory canal passes directly from the frontal to the pterotic (Arambourg 1954: fig. 35). None of these features is seen in *Thrissopater*. The articulation of the quadrate with the mandibular ramus occurs below the middle of the orbit, unlike any species of *Thrissopater* (or *Pachyrhizodus*). The maxilla of *T. daguini* is apparently curved and distally expanded and the teeth on the maxilla and dentary are very small. *T. daguini* is a very small species, the length with the caudal fin being 110 mm (Arambourg 1954: 75) in contrast to all other species. It is clear, from the inclusion of the maxilla in the gape and the form of the postcranial skeleton, that *T. daguini* is a lower teleostean fish but there is little (or perhaps no) evidence justifying its association with *Thrissopater*. *T. daguini* will not be considered further here.

Genus *ELOPOPSIS* Heckel 1856

The genus *Elopopsis* was erected by Heckel (1856), the type species being *E. fenzi* Heckel, from the Cenomanian of Comen, Yugoslavia. Four other species are recognized: *E. microdon* Heckel from the Cenomanian of Yugoslavia and the Lower Cenomanian of Morocco (Arambourg 1954), *E. heckeli* Reuss from the Cenomanian of Czechoslovakia, *E. zieglerei* (Marck) from the Campanian of Westphalia (this form may prove to be conspecific with *E. crassus*) and *E. crassus* Dixon from the *Rhynchonella cuvieri* Zone (Turonian) of Kent, south-east England. Only *Elopopsis crassus* and *E. microdon* are well enough known to deserve comment, and the only species studied in this work is *E. crassus*. The following descriptive remarks are based on seven specimens: BM(NH) P.10217, P.10218, P.10320, P.10337, P.10619, P.11201 and P.11907. All come from the Turonian of south-east England. For diagnoses of this species and the genus see Woodward (1908: 132-133).

DESCRIPTIVE REMARKS. The skull roof is composed of thin bone, unlike *Pachyrhizodus*, to which it is otherwise similar. The roof is broad and in the otic region is convex in the transverse plane. The frontals (Fig. 34, Fr) are large and are marked by prominent growth ridges. Anteriorly the frontals may have overlapped one another. A frontal depression is present, as in *Pachyrhizodus*. The parietals are not seen clearly in any specimen but they appear to have been small with irregular margins and to have been separated by the supraoccipital. The dermethmoid (Fig. 34, De) is very broad and the posterior margin overlaps the frontals in a zigzag fashion. From the underside of the dermethmoid projects a pair of ventrolateral processes, as in *Rhacolepis*. A mesethmoid is present but the limits of this ossification are unknown.

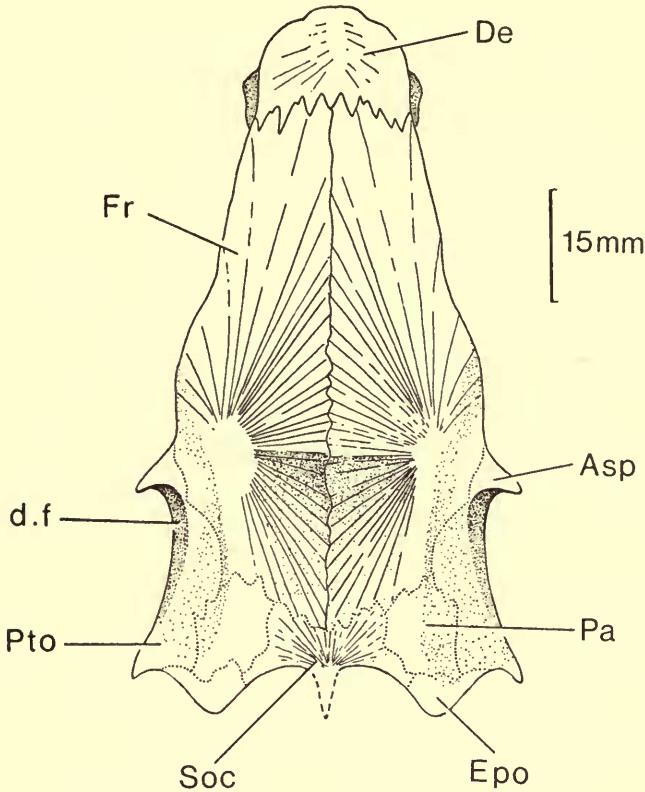


FIG. 34. *Elopopsis crassus* (Dixon). Braincase in dorsal view. Based on BM(NH) P.10218.

The hyomandibular slopes slightly backwards (as in *E. microdon*) in contrast to the vertical hyomandibular of *Pachyrhizodus*. There is a prominent ridge upon the hyomandibular.

There are five infraorbitals known in *E. crassus*. The first is large and is distinctive in that the contained infraorbital sensory canal sends off several branches which radiate from a common origin. The second, which may represent fused second and third infraorbitals, is relatively smaller than the corresponding element in *Pachyrhizodus*. The posterior infraorbitals are rather narrow and do not reach the preoperculum. Narrow posterior infraorbitals may be a specific character of *E. crassus*. *Elopopsis microdon* shows broad posterior infraorbitals (Fig. 35B). The orbit is relatively large in both *E. crassus* and *E. microdon*.

The upper and lower jaws are relatively shorter than in most species of *Pachyrhizodus*. The upper jaw ends beneath the posterior border of the orbit as in *Pachyrhizodus megalops*; the lower jaw ends slightly behind this level. The oral margin of the maxilla is convex and the head of the maxilla is turned slightly inwards and bears a small dorsal ridge which probably articulated with the palatine. There is a single supramaxilla which is relatively broader than that seen 1

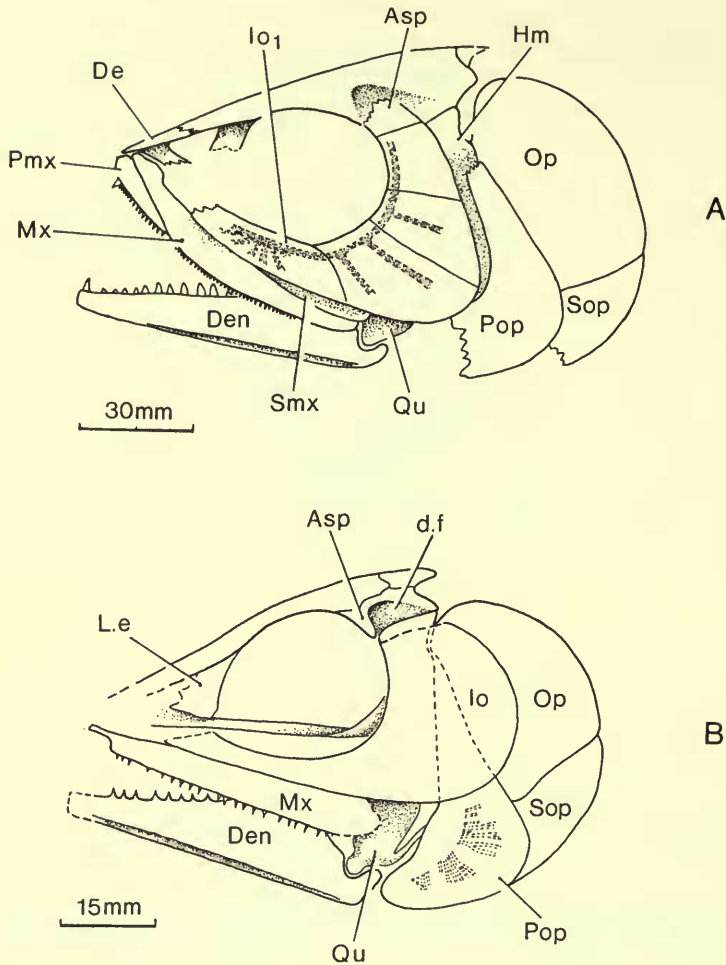


FIG. 35. *Elopopsis*. Outline restorations of the cranium of : A, *Elopopsis crassus* (Dixon) ; B, *E. microdon* Heckel.

Pachyrhizodus. The curved oral margin of the maxilla is not a generic character of *Elopopsis* since *E. microdon* shows a straight maxillary margin as in *Pachyrhizodus*. The premaxilla is triangular and, as Woodward (1908) notes, is expanded horizontally, as in the American species of *Pachyrhizodus*. The mandibular ramus is shallow with a weakly defined coronoid process and is without an inflected ventral margin. Posteriorly, there is a prominent postarticular process.

The dentition has been well described by Woodward (1908). Similarities with *Pachyrhizodus* include prominent inner premaxillary teeth with an outer single row of smaller teeth. The maxilla bears a single row of teeth; the dentary also bears a single row of teeth throughout most of its length but unlike *Pachyrhizodus* there is an enlarged symphyseal tooth. The inner premaxillary teeth and the teeth on the

dentary are laterally compressed, a feature never seen in *Pachyrhizodus*. Behind the symphyseal tooth the teeth on the dentary gradually increase in size posteriorly. In *E. microdon* the dentary teeth are of uniform size, although as in *E. crassus* they are laterally compressed.

The anterior ceratohyal is fenestrated, as in *Rhacolepis* and *Notelops*. There are numerous branchiostegal rays, at least 17 of which can be identified in BM(NH) P.10218. The opercular bones are very thin, as in *Pachyrhizodus*, and the preopercular sensory canal is profusely branched.

The scales are large and deeply overlapping, as in *Notelops* and *Rhacolepis*. The posterior field is marked by small pits and many evenly-spaced circuli are present (Woodward 1908 : pl. 28, fig. 4). Above the origin of the pectoral fin the scales are contoured into a groove which receives the outermost fin-ray and the posterior elongation of the lower postcleithrum. In all, the squamation in this area is very similar to that in *Pachyrhizodus salmoneus*.

There are enough facts known to suggest that *Elopopsis crassus* is similar to *Pachyrhizodus*. More detailed information about *E. crassus* is required, however, before an assessment of its relationships with *Pachyrhizodus*, *Notelops* and *Rhacolepis* can be made.

Arambourg (1954) provided some information on the postcranial skeleton of *Elopopsis microdon*, a small species about 300 mm long. The structure of the caudal skeleton and fin is of interest (Arambourg 1954 : fig. 33 ; pl. 7, fig. 3). The base of the first uroneural is somewhat expanded and overlaps much of the first preural centrum. It resembles *Rhacolepis* in the double nature of the third preural centrum in the specimen figured by Arambourg (fig. 33) and in the ornamentation on this and the preceding centrum.

The neural and haemal arches appear fused with the supporting centra. As in *Rhacolepis* the fin-rays cover much of the hypurals and there are both dorsal and ventral caudal scutes. Further resemblances to *Rhacolepis* are the short paired fins, the origin of the pelvics behind the level of the dorsal fin and the very small scales (as in *Rhacolepis buccalis*). *Elopopsis microdon* apparently shows a series of epipleural intermuscular bones, not seen in any of the fishes grouped here as pachyrhizodontoids.

IV. DISCUSSION

(a). Relationships of *Notelops*, *Rhacolepis* and *Pachyrhizodus*

Features of the three genera which are pertinent to discussions of relationship may be listed as follows:

1. Supraoccipital small, supraoccipital crest weakly developed.
2. Nasals small, tubular (unknown in *Pachyrhizodus*).
3. Supratemporal large, scale-like.
4. Dilatator fossa large.
5. Post-temporal fossa roofed.
6. Otic region of the neurocranium fully ossified.
7. Orbitosphenoid and basisphenoid present.

8. Pars jugularis long ; separate lateral openings for the hyomandibular ramus of VII, jugular vein and orbital artery.
9. Hyomandibular with single articulatory head.
10. Hyomandibular ramus of VII leaving the hyomandibular beneath the opercular process and running in a groove on the posterior margin.
11. Endopterygoid with many small teeth.
12. Palatine without a maxillary process.
13. Hyoid bar consisting of anterior and posterior ceratohyals separated by a narrow band of cartilage. Two hypohyals present.
14. Chondral elements of gill arches ossified, remaining separate from the dermal tooth-plates (unknown in *Pachyrhizodus*).
15. Branchiostegals numerous.
16. Opercular apparatus complete, with large suboperculum and interoperculum.
17. Ribs absent from first two vertebrae.
18. Anterior neural arches and parapophyses autogenous.
19. Epineurals fused with neural arches in abdominal region (unknown in *Pachyrhizodus*).
20. Epipleurals and epicentrals absent (unknown in *Pachyrhizodus*).
21. Anterior neural arches formed in separate lateral halves.
22. Mesocoracoid arch present, united ventrally with both the scapula and coracoid.
23. Two postcleithra.
24. Pectoral fin low on flank, with about 16 rays.
25. Pelvic fins abdominal.
26. Inner pelvic radial spine-like, remaining free from the girdle (unknown in *Pachyrhizodus*).
27. Anal fin small and remote.
28. Caudal fin forked, with 19 principal rays (count not known in *Pachyrhizodus*).
29. Scales cycloid, with bone-cell spaces.
30. Second preural centrum bearing a half-length neural spine.
31. Snout consisting of a large dermethmoid and (except in large species of *Pachyrhizodus*) cartilaginous ethmoid.
32. Frontals large, constituting most of the skull roof.
33. Parietals small.
34. Parietal branch of supraorbital sensory canal absent.
35. Occipital condyle formed entirely by basioccipital.
36. Saccular region of neurocranium not inflated.
37. Parasphenoid without teeth.
38. Basipterygoid process absent.
39. Hyomandibular with well-developed lateral process (ridge) adjacent to the opercular process.
40. Upper jaw in which the premaxilla bears a dorsal process (? articular process) ; maxilla fitting tightly against the premaxilla ; single supramaxilla.
41. Circumorbital series in which the supraorbital is very large, a separate antorbital is absent, the second and third infraorbitals are fused together, and the dermosphenotic is very large and contains a posterior branch of the sensory canal.

42. Pectoral splint absent.
43. Pelvic bones meeting posteriorly in a cartilaginous symphysis (unknown in *Pachyrhizodus*).
44. Posterior neural arches, parapophyses and haemal arches fused with centra.
45. Caudal skeleton in which the parhypural is fused with the first preural centrum, the first ural centrum with a compound element representing the first and second hypurals, and there are varying degrees of fusion between upper hypurals.

Features listed against numbers 1-30 are primitive teleostean characters, showing only that the three genera are at a primitive teleostean grade. Features 31-45 are all advanced in some degree over the basic teleostean plan. Of these features 41 and 45 are particularly significant, serving to show that *Notelops*, *Rhacolepis* and *Pachyrhizodus* form a monophyletic group.

The pattern of circumorbitals in pachyrhizodontoids shows several features that are advanced in relation to the basic teleostean condition as proposed by Nelson (1969).^{*} In pachyrhizodontoids there is no separate antorbital, the second and third infraorbitals are fused together, there is a posterior branch of the sensory canal within the dermosphenotic and the latter is in sutural contact with the large supraorbital - an exception to the last feature is seen in *Pachyrhizodus megalops* where the supraorbital and dermosphenotic just touch one another. Additionally, in *Notelops* the fourth and fifth infraorbitals are fused together as in *Gaudryella* Patterson (1970b : 219).

The fate of the antorbital in pachyrhizodontoids (and, indeed, most other 'lower teleosts') is not known. It could have fused with the first infraorbital as in some osteoglossoid fishes (Nelson 1969 : fig. 12) or with the supraorbital, it could have been lost altogether, or it could have fused with the lateral ethmoid (as has possibly happened in *Hiodon*, according to Greenwood & Patterson 1967 : 215). The last possibility is rejected for the pachyrhizodontoids since there is no dermal component in the lateral ethmoid. Comparisons with the osteoglossoids suggest that the antorbital is not fused with the first infraorbital in the same manner. In *Arapaima* and *Heterotis* (Nelson 1969 : fig. 12) the shape of the compound anterior element and the path of the contained sensory canal strongly suggest a fused antorbital and first infraorbital. In pachyrhizodontoids the infraorbital sensory canal runs to the tip of the first infraorbital without turning dorsally. It should be noted at this point that there is no similarity between the circumorbitals of osteoglossomorphs and pachyrhizodontoids. There is no supraorbital in osteoglossomorphs and where there is fusion of the infraorbitals it occurs between the third and fourth members of the series (Nelson 1969). Elsewhere among 'lower teleosts', loss of a separate antorbital is restricted† to euteleosts. Thus, the absence of a separate

^{*} Nelson (1969) was concerned with the canal-bearing bones of the infraorbital series. It may safely be assumed that at least one supraorbital is also present in the primitive teleostean condition. Furthermore, it is suggested that the primitive supraorbital is a small splint-like element. This, at least, is its form in the vast majority of 'lower teleostean' fishes and in pholidophorids (Nybelin 1966).

† It is possible that the antorbital of some eels has been fused with ethmoid bones since the snout of many eels is a highly consolidated structure. However, there is a separate antorbital in *Simenchelys parasiticus* (McDowell 1973 : fig. 1F), *Synaphobranchus* (Robins 1971 : fig. 1) and in *Atractodenchelys phrix* and *Dysommia* (Robins & Robins 1970 : fig. 3).

antorbital is noted in *Esox* and *Umbra* (Gosline 1961: 28), *Galaxias* (Gosline 1961: 28; McDowall 1969: fig. 3B), *Retropinna osmeroides* and *Prototroctes maraena* (McDowall 1969: fig. 3A, E), *Gonorhynchus* (Gosline 1961: 28), *Hoplías malabaricus* (Weitzman 1962: 29), *Erythrinus unitaeniatus* (Gregory 1933: fig. 67) and *Opsariichthys hainanensis* (Nelson 1969: fig. 5B). It generally disappears in cyprinids, according to Gosline (1961: 30). In these euteleosts, as in the pachyrhizodontoids, there is no direct evidence that the antorbital has fused with the first infraorbital. It is probable that a separate antorbital has been lost many times within 'lower euteleosts' and this may be related to the absence of a supraorbital nasal diverticulum (see Gosline 1961 for details of this structure).

Fusion between members of the infraorbital series lying below and behind the orbit in 'lower teleosts' has been noted by Nelson (1969). In all cases it involves fusion between the third and fourth infraorbitals of the teleostean morphotype. Pachyrhizodontoids are therefore unusual in showing fusion between the second and third infraorbitals.

The dermosphenotic of pachyrhizodontoids is very large. It covers most of the dilatator fossa and has, in addition to the characteristic Y-shaped division of the infraorbital canal, an additional posteriorly-directed branch (or branches as in the case of *Pachyrhizodus megalops*). The only other 'lower teleosts' in which a similar branch is recorded are some salmonids figured by Nelson (1969: fig. 7): *Salmo gairdneri*, *S. trutta*, *Brachymystax lenok* and *Oncorhynchus nerka*. Such a branch is also present in *Oncorhynchus keta*. Elsewhere among 'lower teleosts' there is either no posterior branch-opening in the dermosphenotic or the opening occurs at the junction of the fifth infraorbital with the dermosphenotic.

A large supraorbital which is sutured with the dermosphenotic as in the pachyrhizodontoids is relatively rare in lower teleosts, although it is seen in some characins and catfishes. No phylogenetic inferences may be drawn from this similarity.

In sum, the circumorbital series of the pachyrhizodontoids is distinctive in showing fusion between the second and third infraorbitals and the large size of the dermosphenotic and posterior infraorbitals. Where similarities exist with other 'lower teleosts' these are shared with euteleosts. However, there is no one particular group of euteleosts that is directly comparable with pachyrhizodontoids in this respect.

The caudal skeleton is known (at least, in part) in *Notelops*, *Rhacolepis* and the American species of *Pachyrhizodus* (Fig. 36; Hay 1903: pl. 3; Nelson 1973a: fig. 8A). In these forms the caudal skeleton shares important similarities in the pattern of fusion which appears to be unique among 'lower teleostean' fishes.

The parhypural, which bears a small hypurapophysis in *Rhacolepis* and *Pachyrhizodus*, is fused with the first preural centrum. The first and second hypurals are fused together and to the first ural centrum. There may also be some degree of fusion between the upper hypurals. Fusion between members of the hypural series is probably of little significance since it is subject to individual variation and may even be an ontogenetic phenomenon. It is a common occurrence in euteleosts. Fusion of lower hypurals and the parhypural with supporting centra is common throughout euteleosts but I know of no instance in which this has taken place without prior fusion between the first ural centrum and the first preural centrum.

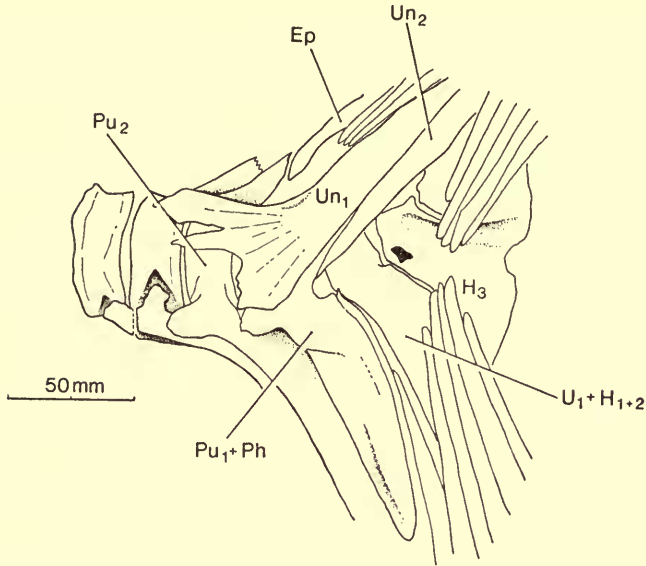


FIG. 36. *Pachyrhizodus caninus* Cope. Freehand sketch of the caudal skeleton as represented in SMU 62406.

Outside the euteleostean fishes fusion between the parhypural and supporting centrum is rare but is recorded in the osteoglossomorphs *Hiodon alosoides* (Gosline 1960 : fig. 4 ; Patterson 1968 : fig. 11) and *Notopterus notopterus* (Nelson 1969 : fig. 20D), and in the clupeomorphs *Denticeps* (Greenwood 1968 : fig. 29), *Ornategulum* and *Diplomystus analis* (Forey 1973a : figs 7, 9A). Fusion of the second hypural with the supporting centrum is characteristic of clupeomorphs (and ostariophysans), but in these fishes this fusion is associated with the freeing of the first hypural, fusion of the anterior uroneural with the first preural centrum and a rather long second ural centrum. None of these associated features is seen in the pachyrhizodontoid caudal skeleton.

There are usually two uroneurals in pachyrhizodontoids, perhaps three in *Notelops*, the first of which is large and expanded (*Notelops*) or forked proximally (*Rhacolepis* and *Pachyrhizodus*). The proximal forking is particularly well developed in *Pachyrhizodus* (Fig. 36 ; Hay 1903 : pl. 3) and this may be an adaptive feature serving to strengthen the skeleton. The caudal fin of *Pachyrhizodus* is very deep and exhibits a high degree of hypurostegy. The base of the anterior uroneural bears a narrow anterior expansion but this is not as well developed as that expansion associated with the first uroneural ('stegural') of salmonoids or osmeroids. The second uroneural is primitively long, reaching to cover the lateral face of the first ural centrum.

In *Rhacolepis* the first preural neural arch is fused with its supporting centrum ; the condition in *Notelops* and *Pachyrhizodus* remains unknown. Similar fusion is seen in clupeomorphs, ostariophysans and some protacanthopterygians (Patterson 1970b).

In sum, the pachyrhizodontoid caudal skeleton is unique among 'lower teleostean' fishes. It is basically primitive, with the few specialized features being seen most commonly in euteleosts. However, fusion between the first ural and first preural centra, so characteristic of euteleosts, has not taken place in pachyrhizodontoids. In those euteleosts in which these centra are not fused (alepocephaloids, esocoids and salmonids) the parhypural and hypurals are also autogenous (more primitive than pachyrhizodontoids) or there is a well-developed 'stegural' present (esocoids and salmonoids, which are therefore more advanced than pachyrhizodontoids in this respect). Features of these two character complexes (circumorbital series and the caudal skeleton) show that *Notelops*, *Rhacolepis* and *Pachyrhizodus* are their own closest relatives.

Notelops, *Rhacolepis* and *Pachyrhizodus* have traditionally been associated with elopoids (Elopiformes), but apart from many shared primitive characters (nos 1-19 and 21-30 from the list, pp. 183-5) they seem to have little in common with the latter. Among the advanced characters listed for pachyrhizodontoids, nos 31 and 37-39 are known in elopoids. These can hardly be regarded as evidence of close relationship since they are also known, for instance, in protacanthopterygians. More importantly, pachyrhizodontoids are not known to have the elopoid characteristics of rostral ossicles or prenasal ossicles (Gosline 1961, Forey 1973b) or fusion between the angular and retroarticular (Nelson 1973a, b). In many characters (e.g. nos 32-36 and 40-45) pachyrhizontoids are more advanced than elopoids.

Pachyrhizodontoids do not share any uniquely specialized features with osteoglossomorphs (or ichthyodectids) and the typical derived characteristics of osteoglossomorphs (Greenwood 1966, Greenwood *et al.* 1966, Nelson 1969, 1972) are absent from *Notelops*, *Rhacolepis* and *Pachyrhizodus*.

Similarly, pachyrhizodontoids do not show any clupeomorph characteristics (for these see Greenwood 1968, Greenwood *et al.* 1966, Patterson 1970a) or the occipito-cervical vertebral and rib specializations of the Ostariophysii (*sensu* Rosen & Greenwood 1970) and cannot be considered closely related to either of these superorders.

The remaining 'lower teleostean' group is the Protacanthopterygii, containing only the Salmoniformes. Unfortunately, it is at present impossible to define the Protacanthopterygii satisfactorily, or to suggest the interrelationships between the constituent members (Patterson 1970b). For this reason it is difficult to justify the inclusion of the pachyrhizontoids within the Salmoniformes (or, for that matter, to justify their exclusion). Within the salmoniforms the Salmonoidei, and in particular the Salmonidae, appear to have retained the greatest number of primitive teleostean characters, but this does not mean to say that they are the 'basal stock', as has been assumed, e.g. by McDowall (1969: 817). A comparison between pachyrhizodontoids and protacanthopterygians shows that there are similarities in certain 'advanced' features, i.e. those thought not to be present in the basic teleostean plan. In some features a resemblance is noted to the large-mouthed salmonids (the salmonines).

Certain features (nos 31-38 listed above, p. 184) are commonly found in protacanthopterygians, and in particular there is a general resemblance between the skull roof of *Rhacolepis*, *Pachyrhizodus* and the salmonines. These resemblances include

the large dermethmoid which is rather blunt anteriorly, the very large frontals and the small, separated parietals. Of the characters nos 31–38, only 35 is not known to occur in all salmonids since, according to Cavender & Miller (1972 : 30), salmonines show a tripartite occipital condyle, which is presumably more primitive than a condyle formed by the basioccipital alone. The resemblances in the skull roof must be due to convergence or, at best, parallelism, since *Notelops* is more primitive in showing medially united parietals, a subtemporal fossa and a prootic–intercalar bridge.

In the hyopalatine series Patterson (1970b) notes the absence of ectopterygoid teeth in all salmoniforms, although there is some doubt as to whether they are absent in *Retropinna* (Weitzman 1967, McDowall 1969); this is an undoubtedly derived character. Among the pachyrhizodontoids *Rhacolepis* shows ectopterygoid teeth. In *Notelops* the toothed palatine has grown back to replace functionally the ectopterygoid as in many salmoniforms.

The upper jaw of the pachyrhizodontoids shows some similarity with that of salmonines (Fig. 37, and see illustrations in Norden 1961 and Vladykov 1962). In both the premaxilla is small and bears a dorsal process (the articular process in salmonids). The maxilla has a simple head, a poorly developed palatine process (absent in some) and a long 'blade' with a small, splint-like supramaxilla. The dentition is also similar, with a series of robust teeth set in pleurodont fashion. The premaxilla of salmonines may bear inner teeth.

The anatomy of the lower jaw of pachyrhizodontoids is somewhat variable. Since the anatomy of the lower jaw of 'lower teleostean' fishes has been the subject of recent discussion by Nelson (1973a, b) it is appropriate to discuss the lower jaws of *Notelops*, *Rhacolepis* and *Pachyrhizodus* in the broad terms of reference he provided. Nelson discusses three aspects of the lower jaw which he found to be subject to some variation – the composition of the articulatory facet, the pattern of fusion between the bones at the posterior end of the jaw and the position of the sensory canal opening.

With respect to the articulation facet, Nelson (1973a) postulated that the primitive teleostean condition shows the development of the facet on the articular and the retroarticular, e.g. as in *Heterotis*. In the pachyrhizodontoids the retroarticular takes no part in the facet and in this they resemble clupeomorphs, euteleosts and ichthyodectids. In *Notelops* the articulation facet is formed from contributions by the separate articular and angular. In *Rhacolepis* and the American species of *Pachyrhizodus* (Nelson 1973a : fig. 2c), in which the angular and articular are fused together, the articulation facet is formed by both articular and angular contributions.

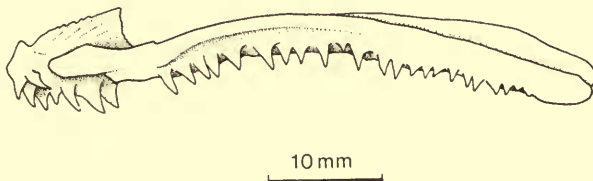


FIG. 37. *Salmo clarki* Richardson. Upper jaw of right side, in medial view.

Thus pachyrhizodontoids are more advanced than the proposed basic teleostean condition in showing an angular (i.e. dermal) contribution to the facet. In this, they resemble clupeomorphs, euteleosts and ichthyodectids and possibly also elopomorphs and ananogmiids (Nelson 1973a).

In *Notelops* the angular, articular and retroarticular are separate ossifications and this is certainly primitive with respect to *Rhacolepis* in which there is a compound angulo-articular and separate retroarticular. The American species of *Pachyrhizodus* are apparently similar to *Rhacolepis* (Nelson 1973a). Conditions in the English species of *Pachyrhizodus* could not be determined because of the lack of suitable material. The unfused condition of the bones in *Notelops* resembles that in certain osteoglossoids and ichthyodectids (Nelson 1973a, b) but since this is presumed to be the primitive teleostean condition no phyletic significance may be inferred from the resemblance. The fusion pattern in the lower jaw of *Rhacolepis* and the American species of *Pachyrhizodus* is similar to that seen in clupeomorphs and euteleosts.

The position of the sensory canal opening in pachyrhizodontoids is not clear. Nelson (1973a) was unable to determine its position in American species of *Pachyrhizodus*. In both *Notelops* and *Rhacolepis* there is a series of pores (only one in the young specimen of *Notelops* shown in Fig. 4) opening onto the lateral surface of the angular (or angulo-articular). The most posterior of these pores lies near the tip of the postarticular process. However, there is also a pore, presumably for the sensory canal, on the medial face of the angular (angulo-articular), located just behind the articulatory facet and in a comparable position to the medial opening in *Elops* and *Megalops* (Nelson 1973a). In *Rhacolepis*, this pore leads to a canal which joins the main mandibular canal at the dentary/angulo-articular overlap. It was not possible to determine where the pore led in *Notelops*. Nelson (1973a) suggested that a medial opening of the sensory canal is a derived teleostean character found in elopiforms, ichthyodectids and ananogmiids. However, Patterson & Rosen (in press) show, in convincing fashion, that the medial opening for the sensory canal is a primitive feature for teleosts and thereby invalidate its use as evidence of relationship.

One further feature of the lower jaw noted by Nelson (1973a, b) is a 'reverse overlap' of the angular and dentary near the coronoid process in elopiforms, characoids and clupeomorphs. Both *Notelops* and *Rhacolepis* show such a 'reverse overlap', which is also seen in the salmonid *Stenodus leucichthys* figured by Cavender (1970 : fig. 7E). The significance of this overlap is not clear.

To summarize the lower jaw evidence in the terms of reference provided by Nelson (1973a, b) : *Notelops* is more primitive than most 'lower teleosts' in showing unfused articular, angular and retroarticular bones ; *Rhacolepis* and the American species of *Pachyrhizodus* resemble clupeomorphs and euteleosts in the fusion pattern. It follows that if *Notelops* is more closely related to *Rhacolepis* and *Pachyrhizodus* than to any other teleost, fusion between the angular and articular must have occurred independently in this lineage as it has apparently in the osteoglossomorph lineage (Nelson 1973b).

A general resemblance may be noted between the lower jaw of *Rhacolepis*, *Pachyrhizodus* and the salmonines (Fig. 38). Resemblances are seen in the dentition,

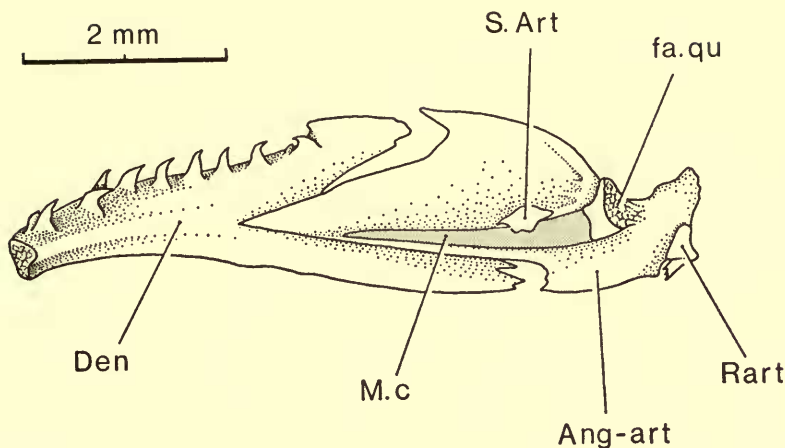


FIG. 38. *Salmo trutta* Linnaeus. Right mandibular ramus of a young individual, in medial view.

the shape and position of the retroarticular and the shape of the articular facet and postarticular process. However, despite these resemblances in shape there is no unique shared derived character that would suggest close relationship.

The pectoral girdle and fin of pachyrhizodontoids are basically primitive and I know of no details here that could be useful in suggesting relationship. The pelvic girdle consists of two pelvic bones that are united posteriorly in a cartilaginous symphysis such as is seen in many protacanthopterygians, including all salmonids. The vertebral column shows fusion between the centra and the posterior parapophyses, haemal arches and the neural arches in the caudal region. Again this is also seen in salmonids where there is also the incipient development of zygapophyses as seen in *Rhacolepis*. Primitively, the pachyrhizodontoid and salmonid vertebral columns lack epicentral or epipleural intermusculars: I have been unable to confirm the presence of epipleurals in *Thymallus arcticus* recorded by Norden (1961).

Despite the osteological similarities between pachyrhizontoids and the salmonines there is no good evidence (i.e. a unique shared derived character) that a close phylogenetic relationship exists. Comparisons between pachyrhizodontoids and the more derived salmoniforms (osmeroids, argentinoids, galaxioids, stomioids, alepocephaloids, giganturoids and esocoids) lead to the same conclusion. In fact, it seems that among the protacanthopterygians the salmonoids are 'closest' to the pachyrhizodontoids, but this is probably only because both are of primitive teleostean grade.

Patterson (1970b) has shown that on the basis of caudal anatomy, the protacanthopterygians may be divisible into two groups. *Rhacolepis* agrees with the alepocephaloid-argentinoid grouping in showing fusion between the first preural neural arch and the supporting centrum, and all pachyrhizodontoids agree with this grouping in lacking a 'stegural' (irrespective of how that structure may be formed).

However, the haemal elements are never fused with centra in the alepocephaloid-argentinoidei group and the full-length second preural neural spine of these fishes is more specialized than the half-length spine of pachyrhizodontoids.

There is probably no advantage to be gained in attempting to compare morphotypes (*sensu* Zangerl 1948) of the Protacanthopterygii and the Pachyrhizontoidei. It would be impossible to establish a protacanthopterygian morphotype on present evidence since, with the possible exception of the toothless ectopterygoid, there are no unifying characters of this group (i.e. monophyly has not been demonstrated) and the interrelationships of the salmoniform suborders are not sufficiently well understood. McDowall (1969) did attempt to deduce a salmonoid morphotype, and since that author believed salmonoids to be the basal protacanthopterygian stock it would also be the salmoniform morphotype, but it proves to be of little use since nearly all the osteological features mentioned are primitive teleostean features. The exception in McDowall's (1969) description of the morphotype is the condition of the snout ossification which was hypothesized using the snout analysis made by Weitzman (1967). Patterson (1970b) justifiably criticizes this analysis, reversing the polarity of the morphocline and resulting in the primitive salmonoid having at least a perichondrally ossified mesethmoid, lateral ethmoids and a separate dermethmoid.

At present, the most that can be said about the relationships of the pachyrhizodontoids is that they are a group of primitive teleostean fishes showing certain derived features seen in euteleostei. However, the Euteleostei cannot yet be critically defined (Nelson 1973a) and therefore there is no logical basis for including the pachyrhizodontoids with an indefinable group. Within the Euteleostei they do not show any ostariophysan features, but do show some resemblance to salmonids. None of these resemblances can be regarded as evidence of relationship. The pachyrhizodontoids cannot be assigned to any existing suborder and must therefore be recognized as possessing, at least, subordinal status and be recognized as Teleostei *incertae sedis*. It is to be noted that Nelson (1973b) recognized *Pachyrhizodus* as Teleostei *incertae sedis*.

(b). Intrarelations and evolution within the Pachyrhizontoidei

From Table 1 (which excludes character states of doubtful phylogenetic significance, e.g. the fenestrations in the dilatator fossa of *Notelops* and the development of the prootic cup in *Pachyrhizodus*) it may be seen that *Rhacolepis* and *Pachyrhizodus* are similar to one another in sharing the derived states of characters 1-2, 4-9 and 12. On this basis *Rhacolepis* and *Pachyrhizodus* are 'sister-groups', but I find it impossible to decide which of the two genera is the apomorph. *Notelops* stands as the plesiomorphic 'sister-group' of *Rhacolepis* and *Pachyrhizodus*. *Notelops* appears to be derived, with respect to the pachyrhizodontids, in two features, the fusion of the fourth and fifth infraorbitals and in character 11 (Table 1). That the pachyrhizodontids have secondarily acquired a short palatine and a toothed ectopterygoid is unlikely, but the possibility cannot be ruled out. In *Rhacolepis* the ectopterygoid bears a single row of pointed teeth which is certainly

TABLE I

Similarities and differences in certain cranial characters between *Notelops*, *Rhacolepis* and *Pachyrhizodus*

	<i>Notelops</i>	<i>Rhacolepis</i>	<i>Pachyrhizodus</i>
1. Parietals	medially united	separated	separated
2. Frontal	lateral margin 'entire'	lateral margin 'excavated' above autosphenotic	lateral margin 'excavated' above autosphenotic
3. Pterotic spine	poorly developed	well developed	poorly developed
4. Subtemporal fossa	present	absent	absent
5. Prootic-intercalar bridge	present	absent	absent
6. Trigeminal foramen	opening into pars jugularis	opening directly to orbit	opening directly to orbit
7. Myodome	closed posteriorly	open posteriorly	open posteriorly (at least in <i>P. megalops</i>)
8. Parasphenoid	shallow beneath otic region	deep beneath otic region	deep beneath otic region
9. Fusion pattern in mandibular ramus	separate angular, articular and retroarticular	angulo-articular and retroarticular	angulo-articular and retroarticular (American species)
10. Dentition in dentary	several rows	single row	single row
11. Palate	palatine long, functionally replacing the edentulous ectopterygoid	palatine short, ectopterygoid with teeth	palatine short, ectopterygoid with teeth
12. Gular plate	present	absent	absent

unlike the presumed primitive teleostean condition in which there is a band of small villiform teeth. The absence of a pterotic spine (character 3, Table I) in *Notelops* and *Pachyrhizodus* is surely a primitive feature. Based on the available facts there is no evidence to refute the suggested phylogeny outlined above. A classification to reflect this hypothesis places *Rhacolepis* and *Pachyrhizodus* in the family Pachyrhizodontidae and *Notelops* in the co-ordinate family Notelopidae.

Accepting the above phylogenetic interpretation (it is the most parsimonious and assumes no parallelism or convergence) certain 'phylogenetic trends' (morphoclines), can be recognized. The skull roof becomes broader, particularly above the orbit, and the frontals increase in relative size. In the otic region of the braincase the roof becomes broader and more convex, the roof of the dilatator fossa becomes very narrow, or absent altogether, above the autosphenotic, the autosphenotic spine increases in relative size and the subtemporal fossa disappears. These changes are probably interrelated and are concerned with the lateral movements of the hyo-mandibular and opercular apparatus. Erosion of the roof of the dilatator fossa and, to a lesser degree, the increase in the size of the autosphenotic spine allow the dilatator operculi muscle to spread dorsally. The increased size of the autosphenotic spine may reflect an increase in the bulk of levator arcus palatini musculature and, because it is located directly above the metapterygoid, is presumably in a position

that would enhance the mechanical advantage of the levator muscle. The loss of the subtemporal fossa is probably related to the broadening and increased convexity of the otic region. In *Elops*, which like *Notelops* has a rather flat skull roof and a subtemporal fossa, the position of the hyomandibular facet relative to the lateral neurocranial wall is such that, were a subtemporal fossa absent, the distance between the medial surface of the hyomandibular and the neurocranial wall would be very short. In *Elops* the adductor hyomandibulae originates from the anterior half of the subtemporal fossa. The development of a subtemporal fossa effectively increases this distance and allows for a greater length (and hence a greater efficiency) of adductor hyomandibulae muscle to be accommodated (Fig. 39). In *Rhacolepis* and *Pachyrhizodus* the hyomandibular facet is drawn away from the lateral neurocranial wall at the level of the adductor origin by a broadening and increased convexity of the skull roof, so space for a suitable length of adductor hyomandibulae muscle is achieved without the need to develop a subtemporal fossa (Fig. 39). Since both structural designs allow for a reasonable length of adductor muscle it is difficult to judge which is the more efficient. However, the subtemporal fossa encroaches upon the lumen of the post-temporal fossa which receives some epaxial musculature. It also restricts the brain and perilymphatic cavities. The *Pachyrhizodus* plan does not impose these restrictions upon these cavities.

In the jaws, the dorsal process of the premaxilla becomes larger, the dentary becomes more robust and an inflected margin develops. The dentition becomes more powerful.

The posterior infraorbitals and the preoperculum become large, covering much of the operculum and suboperculum. The significance of these changes is not known. There is a trend towards an increase in the degree of branching of the preopercular sensory canal.

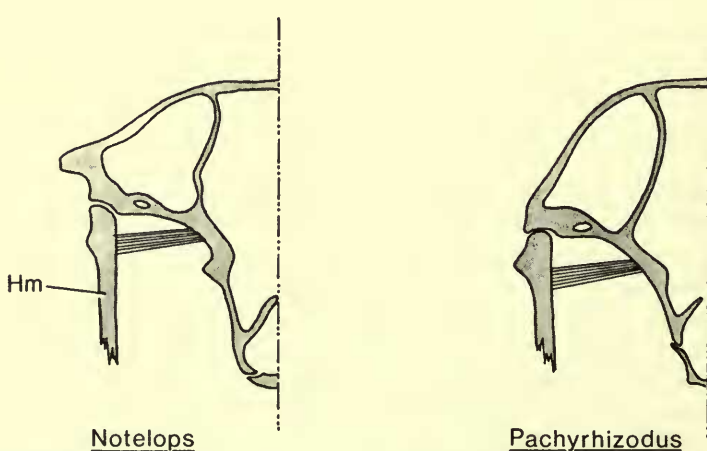


FIG. 39. Transverse sections through the otic region of the braincase and the hyomandibular of *Notelops* and *Pachyrhizodus*, to show the importance of the subtemporal fossa with respect to the length of the adductor hyomandibulae (converging lines).

The pachyrhizodontoids were probably powerful swimmers and were certainly carnivorous. Specimens of *Rhacolepis* contain leptolepid fragments within the abdominal cavity. The caudal fin of the American species of *Pachyrhizodus* is very deep and probably had a high aspect ratio suggesting that these species at least were capable of fast, sustained swimming. The well-developed teeth, distributed mainly on the dermal jaws, and the absence of parasphenoid teeth denote that the primary bite is between the lower and upper jaws, and perhaps the palatine in *Notelops*. This, and the rigidity between premaxilla and maxilla, suggest a feeding mechanism similar to large-mouthed salmonids.

V. SUMMARY

1. Osteological descriptions of *Notelops brama* (Agassiz), *Rhacolepis buccalis* Agassiz and *Pachyrhizodus* [= *Thrissopater*] *megalops* (Woodward) are given. The description of *Notelops brama* is only partial, because Dunkle (1940) has described much of the cranium of this species. Brief notes on the osteology of *Elopopsis*, as represented by *E. crassus* Dixon, are included. *Elopopsis* is thought to be related to *Pachyrhizodus* because of superficial similarities in the skull roof, the dentition, the opercular bones and the squamation at the base of the pectoral fin. Inadequate knowledge of *Elopopsis* precludes further discussion.

2. *Thrissopater* Günther is placed in synonymy with *Pachyrhizodus* Dixon as there is no justifiable basis for separation. The frontal depression, characteristic of *Thrissopater*, is known in *Pachyrhizodus* and the presence of an inner premaxillary tooth, characteristic of *Pachyrhizodus*, is strongly suspected in *Thrissopater*. The English species of *Pachyrhizodus* (including *Thrissopater*) are known mainly by jaw fragments and these species are rediagnosed using these criteria. Other species of *Pachyrhizodus* known from North America and Australia are comparable with the English species (particularly *P. subulidens* and *P. basalis*) in the features of the skull roof, circumorbital and opercular series and in the jaws.

3. *Notelops*, *Rhacolepis* and *Pachyrhizodus* form a monophyletic group, the suborder Pachyrhizodontoidei *nov.*, which is distinguished by features in the circumorbital series (lack of a separate antorbital, fusion between the second and third infraorbitals and the pattern of branching within the dermosphenotic) and the caudal skeleton (separate preural and ural centra, fusion of the parhypural with the first preural centrum, fusion of a compound lower hypural plate with the first ural centrum, a large first uroneural and, at least in *Rhacolepis*, a fusion of the first preural neural arch with the supporting centrum).

4. The combination of derived character states shown by the Pachyrhizodontoidei is most favourably compared to that seen in the Protacanthopterygii. These features are so widely distributed within the protacanthopterygians that it appears impossible to refer the pachyrhizodontoid fishes to any recognized suborder and therefore they must be separated from them at least at the subordinal rank. A general resemblance in features of the skull roof, jaws and vertebral column is noted between pachyrhizodontoids and the large-mouthed salmonids. The Protacanthopterygii and the Euteleostei are, at present, not defined and for this reason the suborder Pachyrhizodontoidei is classified as Teleostei *incertae sedis*.

5. Within the Pachyrhizodontoidei, *Rhacolepis* and *Pachyrhizodus* share several derived character states (e.g. loss of a bone-enclosed ethmoid commissure, separated parietals, loss of the subtemporal fossa and prootic-intercalary bridge, fusion of angular and articular and loss of gular plate) not seen in *Notelops*. *Rhacolepis* and *Pachyrhizodus* are therefore united in the family Pachyrhizodontidae. *Notelops* is placed in the family Notelopidae *nov.* and is considered to be the plesiomorph sister-group of the Pachyrhizodontidae. *Notelops* is probably derived with respect to *Rhacolepis* and *Pachyrhizodus* in showing an elongate, toothed palatine that functionally replaces the ectopterygoid.

VI. ACKNOWLEDGEMENTS

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VII. ADDENDUM

Since the preparation of the final draft of this manuscript, Taverne (1974) has published a paper which includes notes on the systematic position of *Notelops*. Taverne notes similarities and differences between *Elops* and *Notelops* and reaches the conclusion that *Notelops* should be placed in the Salmoniformes, in a new suborder Notelopoidei Taverne. He interprets *Notelops* as a form occupying a phylogenetic position intermediate between elopomorphs and euteleosts (Taverne 1974 : fig. 40).

I would agree with Taverne that *Notelops* shows features that suggest relationship with 'salmoniform' fishes but I fail to see the validity of his arguments. Further, I do not think it wise to place *Notelops* in the Salmoniformes.

Taverne notes that the differences between elopoids and *Notelops* are points of similarity with salmoniforms. Some of these so-called differences are not apparent in any of the specimens used in the preparation of this paper. Thus, two of the differences mentioned by Taverne are the lack of teeth upon the pterygoids and the lack of a buccohypophyseal canal in *Notelops*. All of the specimens of *Notelops* that I have examined show villiform teeth on the endopterygoid and the presence of a buccohypophyseal canal. Furthermore, certain of the differences mentioned by Taverne do not appear to be significant. Thus, Taverne mentions that *Notelops* differs from *Elops* in the presence of a pair of notches, just in front of the ascending

wings of the parasphenoid, for the efferent pseudobranchial arteries. *Elops* is without these notches; *Notelops* is variable as to whether the efferent pseudo-branchial passed through a notch, a foramen or 'marked' the parasphenoid at all. Another difference mentioned by Taverne is the 'well-developed' supraoccipital crest contrasting with the very small crest in *Elops*. It is true that *Notelops* has a proportionately larger crest but the magnitude of the difference does not constitute a significant difference.

Taverne notes the presence of a 'fenêtre auditive' in *Elops*, reputedly absent in *Notelops* (and Salmoniformes). The 'fenêtre auditive' in *Elops* referred to by Taverne is a small triangular space left between the prootic, exoccipital, basioccipital and parasphenoid (Taverne 1974 : fig. 2, *f.b.s.*). In *Elops*, and indeed in the many other fishes which show this feature, the space is covered by membrane. A similar space is shown in some specimens of *Notelops* (Fig. 2, p. 132) and in many young individuals of recent salmonids and ostariophysans. Moreover, it is not present in all species of *Elops* (Forey 1973b : fig. 3). The presence of the gap appears to represent an ontogenetic stage, prior to the full growth of the surrounding bones. The choice of the term 'fenêtre auditive' by Taverne is unfortunate for it in no way represents an auditory fenestra such as is seen in clupeomorphs and *Hiodon*. In these latter fishes this auditory fenestra is between the basioccipital, exoccipital and prootic and is a large oval opening.

Taverne mentions four further differences between *Elops* and *Notelops*. In *Notelops* there are no teeth upon the parasphenoid, the saccular chamber is not inflated, an antorbital is absent and there is fusion between members of the infra-orbital series. I agree with these differences but do not think that they show evidence of particular relationship with the Salmoniformes. It is true that these features are found, in sporadic fashion, within the Euteleostei. Taverne justifiably suggests that elopoids and Salmoniformes belong to the same broad phylogenetic lineage. However, Taverne argues that because *Notelops* differs (some of these 'differences' have been questioned above) from elopoids then *Notelops* must be placed in the Salmoniformes. No good reason is given for placing *Notelops* in the Salmoniformes rather than any other euteleostean group.

Finally, two features of *Notelops* reported by Taverne (1974 : 78) must be corrected. He says that the jaws are edentulous and that there are two supramaxillae. In fact, the premaxilla, maxilla and dentary bear many teeth (see also Woodward 1901, Jordan & Branner 1908, Dunkle 1940) and there is a single splint-like supramaxilla.

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IX. ABBREVIATIONS USED IN FIGURES

Ang	angular	fa.hm	facet for hyomandibular
Ang-art	angulo-articular	fa.pal	facet for articulation with the palatine
Art	articular		
Asp	autosphenotic	fa.qu	facet for articulation with the quadrate
a.t.f.c	anterior opening of jugular canal	f.b.h.c	foramen for buccohypophyseal canal
Bb	basibranchial (numbered 1-3)	f.e.p.a	foramen for efferent pseudo-spiracular artery
Bb.tp ₁₊₂₊₃	tooth plate associated with Bb ₁₋₃	fh	foramen between H ₁ and H ₂
Boc	basioccipital	f.i.c.a	foramen for internal carotid artery
Br.r	branchiostegal ray	f.m	foramen magnum
Bsp	basisphenoid	f.m.c.v	foramen for middle cerebral vein
Cb	ceratobranchial (numbered 1-5)	f.occ.n	foramen for occipital nerve
Ce.a	anterior ceratohyal	f.o.n.a	foramen for orbital artery
Ce.p	posterior ceratohyal	f.p.c	foramen for profundus ciliaris
Cl	cleithrum	f.p.f	foramen leading to post-temporal fossa
Cor	coracoid	Fr	frontal
c.s	caudal scute	f.stt.com	foramen for supratemporal commissure
De	dermethmoid	f.VII.hm	foramen for hyomandibular trunk of VII
Den	dentary	f.VII.ot	foramen for otic branch of VII
d.f	dilatator fossa		
d.l	dorsal (epiotic) limb		
Dsp	dermosphenotic		
Eb	epibranchial (numbered 1-3)	H	hypural (numbered 1-4)
e.com	ethmoid commissure	Hb	hypobranchial (numbered 1-4)
Ect	ectopterygoid	Hm	hyomandibular
Enpt	endopterygoid		
Ep	epural (numbered 1-2)	Ib	infrapharyngobranchial (numbered 1-3)
Epo	epiotic	Ic	intercalar
Exo	exoccipital	il.re	iliac region
		Int	interhyal
fa.eth	facet for articulation with the ethmoid	Io	infraorbital (numbered 1-5)

Iop	interoperculum	Pto	pterotoc
io.s.c	infraorbital sensory canal	Ptt	post-temporal
is.re	ischial region	Pu	preural centrum (numbered 1-4)
L.e	lateral ethmoid	Qu	quadrate
l.l.	lateral line	Rad	radial (numbered 1-4)
M.c	Meckelian cartilage	Rart	retroarticular
M.cor	mesocoracoid	S.Art	sesamoid articular
Mpt	metapterygoid	Sca	scapula
Mx	maxilla	Scl	supracleithrum
Na	nasal	Smx	supramaxilla
NaPu	neural arch associated with preural centrum (numbered)	So	supraorbital
NsPu ₂	neural spine associated with second preural centrum	Soc	supraoccipital
Op	operculum	Sop	suboperculum
Ors	orbitosphenoid	so.s.c	supraorbital sensory canal
Pa	parietal	Stt.com	supratemporal commissure
Pal	palatine	Sy	symplectic
Par	parasphenoid	U	ural centrum (numbered 1-2)
Pcl.d	dorsal postcleithrum	Un	uroneural (numbered 1-3)
Pcl.v	ventral postcleithrum	Ur	urohyal
Ph	parhypural	v.l	ventral (intercalar) limb
Pmx	premaxilla	Vo	vomer
Pop	preoperculum	I	foramen for olfactory tract
Pop.s.c	preopercular sensory canal	III	foramen for oculomotor
p.re	pubic region	IV	foramen for trochlear
Pro	prootic	V	foramen for trigeminal
Psp	pterosphenoid	IX	foramen for glossopharyngeal
p.t.f.c	posterior opening of jugular canal	X	foramen for vagus

X. INDEX

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